THE UTILIZATION OF LITTORAL AND ESTUARINE HABITATS BY FISH IN THE SOUTHWESTERN CAPE

by

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CONTENTS

ABSTRACT

This thesis examines the utilization of rocky intertidal, sandy-beach surf-zone and estuarine habitats by fishes on the southwestern Cape coast of South Africa. It has three central objectives: 1) to determine the species composition, abundance, size structure and seasonality of fish and to examine the extent to which they are influenced by environmental factors; 2) to describe the diets and patterns of feeding of the fish and to assess their impact on the food resources; and 3) to determine the importance of these habitats as nursery areas for juvenile fish. A similar number of species (20-22) were sampled in each habitat but all the rock-pool species were unique to that habitat and estuaries and the surf-zone shared only 10 species. Almost all the rock-pool species were residents and all but one of the surf-zone species were migrants. Estuaries contained both residents and migrants. Seasonal and longer-term variation in the populations of rock-pool fishes was small, in contrast to with both estuaries and the surf-zone, where marked seasonal variation was observed. Rock-pool species fed almost entirely on small benthic invertebrates and surf-zone fish consumed largely zooplankton. Estuarine fish, on the other hand, utilized a much wider variety of food including detritus, aquatic macrophytes, zooplankton, benthic invertebrates and fish. Food resource partitioning was a feature of rock-pool and estuarine fish communities but in neither habitat was total consumption by the fish large in comparison with prey production. Western Cape rocky shores did not serve as a nursery ground and were occupied solely by resident species. Availability of rock cover in pools was the single most important variable limiting species richness, abundance and biomass. The surf zone was dominated by small fish, many of which were juveniles of migrants. The surf zone is clearly of some importance as a nursery area for certain species. Estuaries are physically variable and the reproductive patterns of both resident and migrant fish were geared to periods of winter stress when western Cape estuaries are flooded with fresh water.

INTRODUCTION.

INTRODUCTION

Briggs (1974), drawing on the earlier work of Smith (1945), Stephenson (1948), Day (1967) and Day *et. al.* (1970), recognised three marine faunal provinces around the coast of South Africa. They are the subtropical Western Indian Ocean province which extends down the eastern coast as far as approximately the mouth of the Kei river, the warm temperate Agulhas province which includes the southeastern and southern Cape coasts, and the cool temperate Namaqua province which extends up the western Cape coast. The southwestern Cape coast between Cape Point and Cape Agulhas, the area in which the majority of the work included in this thesis was conducted, was considered to be an area of overlap between the Agulhas and Namaqua provinces.

The utilization by fishes of estuarine habitats on the eastern and southeastern coasts of South Africa has been the focus of considerable recent research. Their origins and zoogeographic affinities have been analysed (Blaber 1981), their species composition, abundance and size structure has been quantified in a large number of estuaries (eg. Wallace 1975a; Winter 1979; Marais & Baird 1980; Blaber & Cyrus 1981; Marais 1983a,b; Beckley 1984; Kok & Whitfield 1986; Whitfield 1988) and the diets, growth rates and reproductive biology of many of the species have been described (eg. Wallace 1975b; Blaber 1974, 1978, 1984; Whitfield & Blaber 1978a,b,c; Wallace & Schlyer 1979; Marais 1984; Cyrus & Blaber 1984; Whitfield 1985). Factors influencing the utilization of estuaries in this geographic region have also been analysed (eg. Wallace & van der Elst 1975; Whitfield 1980a,b, 1983, 1984; Blaber 1981; Blaber *et. al.* 1981; Melville-Smith *et. al.* 1981; Whitfield *et. al.* 1981; Marais 1982; Beckley 1985a; Cyrus & Blaber 1987a,b) and are now fairly well understood.

A considerable amount of work has also been done on rocky-shore fish on the eastern and southeastern coasts. The species composition, abundance and distribution of rock-pool and gulley fish in a number of areas has been quantified (Christensen 1976; Christensen & Winterbottom 1981; Beckley 1985b; Buxton & Smale 1984; Smale & Buxton 1989), the feeding biology of some species has been described (Christensen 1978a,b; Stobbs 1980; Butler 1982), as has recolonization after experimental elimination (Beckley 1985c) and the nursery function of the habitat has been assessed (Beckley 1985b; Smale & Buxton 1989).

Knowledge of the utilization of the surf-zone of sandy beaches in the southeastern Cape is attributable to a series of papers by Lasiak. She sampled the fish assemblage at two beaches in Algoa Bay and reported on their long- and short-term fluctuations (Lasiak 1984a,b), recruitment and growth patterns (Lasiak 1983a), reproductive biology (Lasiak 1983b, 1984c), diets (Lasiak 1984d) and on the implications of the surf-zone habitat for teleost nursery areas (Lasiak 1981,1986).

In contrast to this extensive body of work on the inshore fish of the eastern and southeastern coasts, the situation is very different in the southwestern Cape. Here, work on estuarine and littoral fish has been confined almost exclusively to their taxonomy and distribution. With the exception of the notes on the fish fauna of Sandvlei (Begg 1976) and on the biology of *Rhabdosargus globiceps* in the Kleinrivier estuary (Talbot 1955) there are no published details on the utilization of estuaries by fish in this zoogeographic region. The studies of Marsh *et. al.* (1978), who described the species richness and abundance of clinids in rock-pools, Veith (1979), who described the reproduction of *Clinus superciliosus*, and the unpublished accounts of Jackson (1950) and Penrith (1965) who provided notes on the distribution, diets and reproduction of some rock-pool species, are the only data available that concern the fish of western Cape rocky shores. There is no

information on the biology of fish occupying the surf-zone of sandy beaches in this region. Thus the utilization by fishes of estuarine and littoral areas in the southwestern Cape was poorly understood prior to the inception of the papers presented in this thesis. The major aim of the thesis is to rectify this situation, focusing on three central objectives:

1. To determine the species composition, abundance, size structure and seasonality of fish in rocky intertidal, surf zone and estuarine habitats in the southwestern Cape and to examine the extent to which they are influenced by environmental factors.
2. To describe the diets and patterns of feeding of the fish in these habitats in order to assess their impact on the food resources.
3. To assess the importance of these habitats as nursery areas for juvenile fish.

To achieve these objectives twelve key questions were formulated:

1. What species occur in the intertidal zone of rocky shores in the southwestern Cape, what is their abundance and size structure and what factors govern the distribution and abundance of the resident species?
2. What are the fish of the rocky intertidal eating and how do they subdivide their food resource between them?
3. What is the role of resident fish in terms of energy transfer through the rocky shore ecosystem and is food availability likely to be limiting their populations?
4. How do rock-pool fish communities vary around the Cape coast and how important is this habitat as a nursery area?
5. What is the species composition, abundance and size structure of fish in the surf zone of sandy beaches, how do they vary through the year and how important is the surf zone as a nursery area?

6. What is the species composition abundance, size structure and seasonality of fish in southwestern Cape estuaries and how might differences in these estuarine fish communities be explained?
7. How important are estuaries as nursery areas for juvenile fish on the coast of South Africa?
8. What effects do mouth state and the duration of closure have on the structure of the fish community of estuaries such as the Bot that are prone to prolonged isolation from the sea.
9. What is the relative susceptibility of estuarine fish to hyposalinity, as exemplified by the Bot estuary, and what management options might prevent fish kills by low salinities?
10. What are the diets of the fish species inhabiting southwestern Cape estuaries and how do they vary with size and season?
11. Is there any evidence that estuaries offer better feeding conditions to fish than the adjacent marine environment?
12. What are the relationships between prey production and consumption by fish in estuaries, and what do these relationships reveal about the importance of fish as predators in the systems and about the role of niche apportionment as a means of reducing competition?

OVERVIEW OF THE RESEARCH

The key questions outlined above are each addressed separately in the thirteen papers that that form the bulk of this thesis. A brief resume of these papers follows.

Rocky intertidal

1. Factors affecting the distribution, abundance and diversity of rock-pool fishes on the Cape Peninsula, South Africa. *South African Journal of Zoology* **19**: 97-104.

A quantitative description of the fish communities inhabiting rock-pools at three sites, and the relationships between the physical charactaristics of the pools and the distribution, abundance and diversity are given. A total of 1541 fish, representing 21 species were collected from 84 pools using the ichthyocide Rotenone. The number of species, number of individuals and biomass of fish in the pools all correlated significantly ($p < 0.01$) with pool size, the amount of rock cover available and height on the shore. These three environmental variables in combination accounted for between 58% and 88% of of the observed variance in the fish community, with rock cover, which explained up to 76% of the variance, being the single most important variable.

2. The diets of littoral fish from the Cape Peninsula. *South African Journal of Zoology* **18**: 343-352.

The stomach contents of 1929 individuals of 20 species of fish collected from rocky littoral areas in the southwestern Cape were analysed with the objective of ascertaining which food resources were most heavily exploited and the extent of competition between the co-habiting species. Three prey types, amphipods, isopods and polychaetes, occurred in the diets of almost all species and together they comprised more than half the total quantity of food consumed by 14 of the species. Despite this dietary overlap there was considerable subdivision of the resource, much of which was explained in terms of horizontal and vertical differences in fish distribution, habitat preferences, mouth sizes and changes in diet during growth.

3. A population energy budget for *Clinus superciliosus* L., with an assessment of the role of resident fish as predators in the intertidal zone. *Marine Biology Letters* **5**: 323-334.

Laboratory experiments were undertaken in order to quantify the different components of the energy budget for *Clinus superciliosus*, the dominant intertidal fish species on southwestern Cape shores. By extrapolating the results obtained in the laboratory it was estimated that the naturally occurring population consumes 111 kJ $m^{-2}y^{-1}$ and that all resident intertidal fish consume 345 kJ $m^{-2}y^{-1}$. Total invertebrate production on the shore is estimated as 14 592 kJ $m^{-2}y^{-1}$ thus the fish community are consuming in the region of 2.4% of production. Only 538 kJ $m^{-2}y^{-1}$ of production is, however, in the form of the small crustaceans, molluscs and polychaetes normally consumed by these fish. Thus they may exert considerable predation pressure on their prey.

4. The rock-pool fish community of Koppie Alleen and an assessment of the importance of Cape rock-pools as nurseries for juvenile fish. *South African Journal of Zoology* **22**: 25-32.

Fishes inhabiting rock-pools on the southern Cape coast were sampled quarterly over two years. A total of 2595 fish of 21 species representing nine families were collected. Comparisons with the eastern and western Cape fish faunas revealed eastward increases in the total number of species, in the number of subtropical species, and in the contribution of transient species, but a decrease in the resident component. The importance of the Cape rock-pool habitat as a nursery area was assessed by comparing the numbers of juvenile transient species in rock-pools with available information on other inshore habitats. No species were found to be

entirely dependent on Cape rock-pools as a juvenile nursery area although five species appeared to make some use of this habitat.

Surf-zone

5. The fish community of a moderately exposed beach on the southwestern Cape coast of South Africa and an assessment of this habitat as a nursery for juvenile fish. *Estuarine, Coastal and Shelf Science* **28**: 293-305.

The ichthyofauna of a moderately exposed surf-zone habitat on the southwestern Cape coast was sampled by seine netting monthly for 13 months. Twenty species of fish, 40 306 individuals weighing 211 kg, were captured. The number of species and standing crop varied seasonally with higher values during the summer. Four species were present throughout the year, eleven occurred seasonally and the remaining five sporadically. Eighteen of the species occurred almost exclusively as juveniles and only two as adults. Comparison of the abundance of juveniles in the surf-zone with other inshore marine habitats suggested that five species may be entirely dependent and three species largely dependent on the surf-zone as a nursery area.

Estuaries

6. A comparison of the fish communities in nearby permanantly open, seasonally open and normally closed estuaries in the southwestern Cape. *South African Journal of Marine Science* **8**: 43-55.

Seine netting for 13 consecutive months in the permanantly open Palmiet estuary, in the seasonally open Kleinmond estuary and in the Bot estuary, which had been closed for three years, yielded 101 000 fish. Classification and ordination showed

that the structure of the fish communities changed markedly through the year in the Palmiet and Kleinmond estuaries but not in the Bot. Differences in species composition and seasonality in the three estuaries were related to the spawning seasons of the resident and migrant species and to differences in the duration of the connection between the estuaries and the sea.

7. *Clinus spatulatus*, a new species of clinid fish (Perciformes: Blennioidei) from South Africa, with a modified definition of the genus *Clinus*. *Special publications of the J.L.B. Smith Institute of Ichthyology* **29**: 1-9.

During the ecological studies of fish inhabiting southwestern Cape estuaries an undescribed species of clinid was discovered. This paper describes *Clinus spatulatus* sp. n. from 50 specimens collected in the Bot estuary and provides some details on its biology and ecology.

8. South African estuaries and their importance to fishes. *South African Journal of Science* **80**: 203-207.

This paper reviews all available information concerning the utilization by fish of estuaries around the South African coast. The abundance of the different species in estuaries relative to other marine habitats is analysed and fish fauna is divided into six categories according to the extent of their apparent dependence on estuaries. Eight species are considered to be entirely dependent on estuaries throughout their entire life cycles and 22 species are wholly or largely dependent on estuaries as juveniles. Approximately 50 species apparently benefit from the estuarine nursery area. More than 100 other species have been recorded in South African estuaries but these are considered as "strays" or "miscellaneous" species.

9. Changes in the fish fauna of the Bot River estuary in relation to opening and closure of the estuary mouth. *Transactions of the Royal Society of South Africa* **45**: 449-464.

The fish community of the Bot estuary was sampled with gill and seine nets between April 1980 and July 1983. During part of this period the estuary, which is usually closed, was in contact with the sea via an artificially opened deep-water mouth as well as a natural spillway into the adjacent Kleinmond estuary. The changes in the species composition, abundance and size structure of the fish community that occurred as a result of these connections with the sea are described, as are the seasonal and longer-term changes that occurred during the closed phase. The implications of opening the mouth, for the fish and the fishermen that utilize the lagoon, are outlined and management options discussed.

10. A mass mortality of fish associated with low salinity conditions in the Bot River estuary. *Transactions of the Royal Society of South Africa* **45**: 437-447.

In October 1981, after four years of isolation from the sea, the maximum salinity in the Bot estuary fell to 3‰ resulting in a mass mortality of fish. Counts of the dead fish that washed up on the shore around the estuary were made and the extent of the fish kill was compared with the species composition and relative abundance of fish prior to the mortality and with published records of the minimum salinities that the species were previously known to tolerate. Management of the estuary is discussed in the light of the findings.

11. The diets of fish in three southwestern Cape estuarine systems. *South African Journal of Zoology* **24**: 163-177.

The stomach contents of 2 756 fish of 14 species taken by gill and seine nets in the Bot, Kleinmond and Palmiet estuaries were examined. Seven of the species were carnivores which fed primarily on invertebrates, two were herbivores, two were piscivores and three were omnivores. The small juveniles of all species consumed primarily zooplankton. Within these trophic groupings variations in the diets of fish from the different estuaries were noted as were changes in diet with season. Differences between estuaries were ascribed primarily to food availability and differences in the size ranges of fish sampled in them. The estuarine food chain supporting the fish is based primarily on detritus.

12. A comparison of the physiological condition of the southern mullet *Liza richardsoni* (Smith) in a closed estuary and the sea. *Transactions of the Royal Society of South Africa* **45**: 427-436.

The physiological condition of samples the mullet *Liza richardsoni* from the closed Bot estuary was compared with that of the same species sampled in the sea. Protein and ash levels were similar in both estuarine and marine fish but lipid and energy levels were higher, and the water content lower, in the estuarine samples. This species does not spawn in estuaries thus its better condition there may be attributed to the retention of energy usually lost to spawning in the sea. Estuarine juveniles were, however, also in better condition indicating that improved feeding conditions were available in the estuary.

13. Relationships between production and consumption of prey species by resident fish in the Bot, a cool temperate South African estuary. Submitted to *Estuarine, Coastal and Shelf Science*.

Data on the biomass, diets, feeding cycles and consumption rates of the resident fish of the Bot estuary are presented, together with figures for the biomass and

production of invertebrates. While the estuary was closed consumption by the fish accounted for 17% of secondary production or 30% of the production of the prey species, suggesting that predation by fish was not likely to be having a major impact on the prey resource and that food was not in short supply. After the estuary was opened to the sea prey biomass was much reduced and fish biomass increased resulting in an increase in the consumption by fish to some 90% of production. Thus, at this time, competition for food between the fish was probably intense. Dietary niche breadth was correlated directly with abundance, but bore no relationship to mean overlap with other species. Dietary specialization therefore seems of dubious value as a means of reducing competition.

STATEMENT OF RESPONSIBILITY

The above papers are the sole responsibility of the the candidate although three of them are co-authored by either Profs. G.M. Branch or C.L. Griffiths, the joint supervisors of this project. Exceptions are the two papers on which H.P. de Decker and J.H. Wallace are the senior authors (Chapters 12 & 8 respectively). The first of these papers, "A comparison of the physiological condition of the southern mullet ...." was conceived and closely supervised by the candidate while the analyses were undertaken by de Decker who submitted the work as an honours project and subsequently published it. The paper on which J.H. Wallace is the senior author was written as the result of a workshop on the importance of estuaries to fishes in South Africa. The candidate was a participant at this workshop and provided the data for the western and southwestern coasts and was actively involved in the preparation of the manuscript.

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CHAPTER 1.

Factors affecting the distribution, abundance and diversity of rock-pool fishes on the Cape Peninsula, South Africa

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A quantitative description of the fish communities inhabiting rock pools on the Cape Peninsula, South Africa, and the relationships between the physical characteristics of the pools and the distribution, abundance and diversity of the resident fish fauna are given.

A total of 1 541 fish, representing 21 species, were collected from 84 rock pools using the ichthyocide Rotenone. The mean density was 7,42 fish m^{-2} (49,60 g m^{-2}) of pool area or 0,58 fish m^{-2} (3,67 g m^{-2}) of the whole intertidal zone in which the pools were situated. *Clinus superciliosus, C. cottoides* and *Chorisochismus dentex* were the most abundant species, together comprising 75% of the biomass and 60% of the number of fish caught.

The number of species, number of individuals and biomass of fish in the pools all correlated significantly ($P < 0,01$) with pool size and the amount of rock cover available. In addition, the number of species decreased up the shore. These three environmental factors in combination accounted for between 58% and 88% of the observed variance in diversity, number and biomass of fish in the pools. Rock cover was the single most important variable, explaining up to 76% of the variance. Possible reasons for the importance of rock cover and its relationship with pool size, are discussed.

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'n Kwantitatiewe beskrywing van die visgemeenskappe wat in die rotspoele van die Kaapse Skiereiland voorkom, word gegee en die verhoudings tussen die fisiese eienskappe van die poele en die verspreiding, getalsterktes en diversiteit van die visfauna is ondersoek.

'n Totaal van 1 541 visse van 21 spesies is uit 84 rotspoele met behulp van die visgif Rotenone gekollekteer. Die gemiddelde digtheid was 7,42 visse m^{-2} (49,60 g m^{-2}) van die poel-area, of 0.58 visse m^{-2} (3,67 g m^{-2}) van die hele getysone waarin die poele voorkom. *Clinus superciliosus, C. cottoides* en *Chorisochismus dentex* was die volopste spesies en het saam 75% van die biomassa en 60% van die getal visse wat gevang is, gevorm.

Die aantal spesies, aantal individue en biomassa van die visse in die rotspoele het betekenisvol gekorreleer ($P < 0,01$) met poelgrootte en die hoeveelheid rotsbedekking beskikbaar. Daarby het die aantal visse teen die strand op verminder. Hierdie drie omgewingsfaktore saam was verantwoordelik vir tussen 58% en 88% van die variasie wat waargeneem is in die diversiteit, getalle en biomassa van die vis in die poele. Die belangrikste enkele veranderlike was rotsbedekking wat tot 76% van die variasie kon verduidelik. Moontlike redes vir die belangrikheid van rotsbedekking en die verhouding daarvan met poelgrootte word bespreek.

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Existing literature on the biology of intertidal fish has been comprehensively reviewed by Gibson (1969, 1982) who points out that relative to other elements of the intertidal community, fish have received remarkably little attention. Most studies on fish have, moreover, dealt with the northern hemisphere while African, Australian and South American shores remain poorly known.

General information on the species composition, relative abundance and intertidal zonation of fishes inhabiting rock pools in the south-western Cape Province, South Africa, is given by Jackson (1950) and Penrith (1965). Neither report was published, nor provided measures of absolute abundance.

Factors regulating density and species composition of rock-pool fish communities in South Africa and elsewhere remain virtually unknown (Gibson 1982). Seasonal changes in diversity occur and can be correlated with seasonal fluctuations in temperature, wave action and upwelling intensity (Green 1971; Grossman 1982; Thomson & Lehner 1976). South-western Cape rock-pool fish populations remain stable in the long and short term (Jackson 1950; Penrith 1965, 1970) perhaps because there is little seasonal variation in water temperature (Griffiths 1977; Penrith 1970).

In this study, we provide the first quantitative estimates of the abundance and composition of South African intertidal fish communities and elucidate the physical attributes of rock pools that influence the number and species of fish. The feeding habits of the fish collected during this study are reported elsewhere (Bennett, Griffiths & Penrith 1983).

Methods

Samples were collected from six intertidal localities around the Cape Peninsula, South Africa; three in False Bay and three along the West Coast (Figure 1). Each site was visited at low water of spring-tide (LWS) between July and September 1982 and pools representative of the full height and size range were selected. The height (HGHT) and distance (DIST) of each pool from the LWS mark were recorded and its area (AREA), maximum depth (MAXD) and mean depth were measured. Pool volume (VOL) was calculated by multiplying mean depth by area. Subjective ratings of rock (ROCK) and algal (WEED) cover available as shelter to the fish were made on a scale of zero to ten. Total pool area (including pools that were not sampled) in 20 m wide transects was measured and expressed as a percentage of the total area included in each transect.

After Rotenone (dissolved in acetone) had been added to the pools, fish were collected with hand-nets and immediately transferred to 10% formalin. Each fish was subsequently iden-

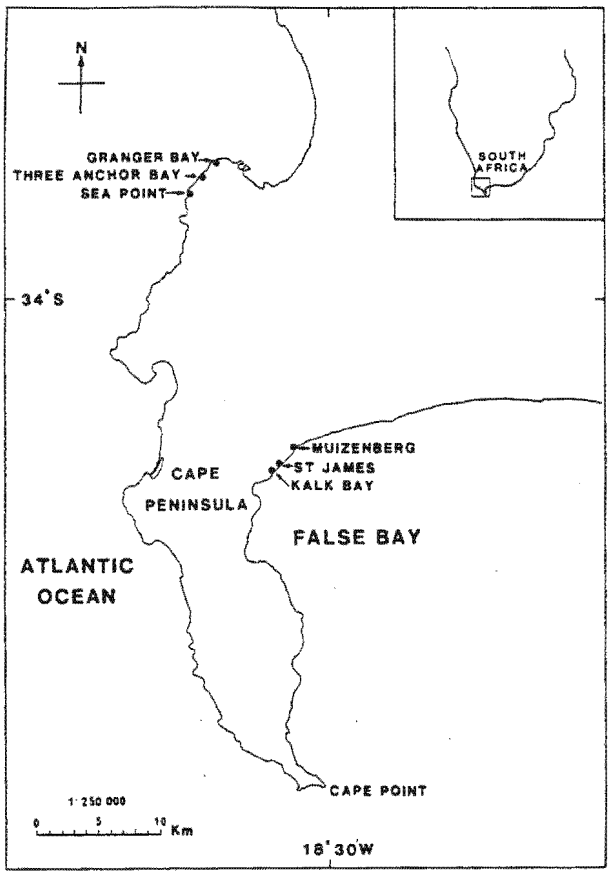

Figure 1 Cape Peninsula, South Africa, showing the six sites from which rock-pool fish were sampled.

tified to species according to Penrith (1969) for clinids and Smith (1965) for other species, measured to the closest millimetre (total length) and weighed to within 0,01 g (wet mass).

Data analysis

Simple linear regression analysis was performed on all possible two-way combinations of dependent variables (number of species, number of fish and biomass) and independent variables (HGHT, DIST, AREA, VOL, MAXD, ROCK and WEED). The respective correlation coefficients were tested for significance ($H_0 : r = 0$; $H_1 : r \neq 0$) and bivariate scatter plots were examined to detect strongly deviating data.

Stepwise multiple regression analyses were used to determine which of the environmental factors significantly contributed to an explanation of the variance in the dependent variables. At each step in the regression, the independent variable with the highest partial correlation coefficient was entered into the equation. Partial correlation coefficients were then recalculated and the procedure repeated until the equation contained all (and only) variables with significant partial correlation coefficients ($P < 0,05$). Significance levels were determined by partial F-value, using a one-sided test and t-value using a two-sided test. The computer program used was STEPREG 1 (Allen 1973) of the STATJOB series.

Multiple coefficients of determination (r^2) were used as an index of predictive value since they are considered to be the amount of variability in the dependent variables accounted for by correlating them with one or more of the independent variables (Zar 1974).

Linear, log-linear (dependent variable transformed), linear-log (independent variable transformed) and log-log models were used for two reasons: firstly, the data were in some cases not normally distributed and secondly, to detect possible non-linear relationships between the variables.

Unless otherwise stated, where pairs of figures are given in the text, the order is always False Bay : West Coast.

Results and Discussion

The fish communities

A total of 1 541 fish representing 21 species were collected from 84 rock pools (Table 1). Sampling effort was greater on the West Coast where 1 028 fish with a biomass of 6 286 g were collected from 50 pools. In False Bay, 34 pools yielded 513 fish with a mass of 4 021 g. Population densities on the two sides of the Peninsula were very similar, both numerically (6,82 and 7,75 fish m^{-2} pool area) and in terms of biomass (53,45 and 47,41 g m^{-2} pool area). When calculated in terms of the whole shore area in which the pools were situated, densities were again similar: 0,55 and 0,60 fish m^{-2}; 4,30 and 3,20 g m^{-2}.

It is very difficult to compare these figures with any of the previously published information on the densities of rocky shore fish populations elsewhere. Gibson (1982) provides a table of such figures and discusses the problems facing different authors in their choice of units for expressing density. In view of the lack of available information concerning factors as the number of pools per unit shore area, pool size distribution, the proportion of fish inhabiting areas other than rock pools and the proportions of cryptic as opposed to free-swimming species, detailed comparisons are not possible. It suffices to say that Gibson's (1982) observation that 'densities rarely exceed a few individuals per square metre' also holds true for the south-western Cape.

Species distribution and abundance varied considerably between the two sides of the Peninsula. Eight species were common to both sides with eight restricted to False Bay and five to the West Coast (Table 1). The greater number of species in the False Bay sample (despite the smaller sampling effort) reflects the general trend in diversity of intertidal species between the two sides of the Peninsula (Stephenson 1939, 1944, 1948) and has been demonstrated in the Clinidae by Penrith (1970).

Abundance values for False Bay, for the West Coast and for the combined data are shown in Table 1. *Clinus cottoides* was numerically the most important species on the False Bay coast, followed by *Caffrogobius caffer, Clinus superciliosus* and then *Chorisochismus dentex*. In terms of biomass, however, *Clinus superciliosus* dominated the catches followed by *Caffrogobius caffer, Clinus cottoides* and then *Chorisochismus dentex*. On the West Coast, the abundance hierarchy was different. *Clinus superciliosus* dominated in terms of both numbers and biomass with *Clinus cottoides* and *Chorisochismus dentex* being the second and third most important species numerically. The same two species also filled the second and third places in terms of biomass, but in the reverse order. When the West Coast and False Bay data are combined, *Clinus superciliosus, Clinus cottoides* and *Chorisochismus dentex* are the most abundant species, together comprising 75% of the total biomass and 60% of the total number of fish caught.

Zonation

The intertidal distribution and abundance of the various species occurring on each side of the Cape Peninsula are shown in Figures 2 and 3. In the case of those species which occur on

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Table 1 The abundance and biomass of fish collected from intertidal rock pools around the Cape Peninsula

	False Bay		West Coast		Combined data	
	$N\ m^{-2}$	$g\ m^{-2}$	$N\ m^{-2}$	$g\ m^{-2}$	$N\ m^{-2}$	$g\ m^{-2}$
Ariidae (sea catfishes)						
Galeichthyes feliceps (Valenciennes)	0,05	0,40	–	–	0,02	0,14
Cheilodactylidae (fingerfins)						
Cheilodactylus fasciatus Lacépède	0,01	0,42	–	–	<0,01	0,15
Congrogadidae (snakelets)						
Halidesmus scapularis Günther	0,24	0,74	–	–	0,09	0,27
Clinidae (klipfishes)						
Blennioclinus brachycephalus (Valenciennes)	0,03	0,09	0,02	0,07	0,02	0,08
Clinus acuminatus Bloch-Schneider	0,12	2,13	0,71	1,60	0,50	1,79
C. agilis Smith	–	–	0,65	1,70	0,41	1,08
C. anguillaris (Valenciennes)	0,12	3,07	0,06	0,70	0,08	1,56
C. berrisfordi Penrith	0,08	0,83	–	–	0,03	0,30
C. brevicristatus Gilchrist & Thompson	–	–	0,01	0,03	<0,01	0,02
C. capensis (Valenciennes)	0,21	1,68	–	–	0,08	0,61
C. cottoides Valenciennes	2,37	10,72	1,09	6,46	1,55	7,96
C. dorsalis Castelnau	0,19	0,30	0,84	0,53	0,60	0,45
C. heterodon Valenciennes	–	–	0,47	1,49	0,30	0,95
C. superciliosus (Linnaeus)	1,34	15,44	2,61	22,08	2,15	19,68
C. taurus Gilchrist & Thompson	0,01	0,16	–	–	<0,01	0,06
C. venustris Gilchrist & Thompson	–	–	0,12	0,27	0,08	0,17
Pavoclinus mus (Gilchrist & Thompson)	0,03	0,22	–	–	0,01	0,08
P. pavo (Gilchrist & Thompson)	0,04	0,28	–	–	0,01	0,10
Gobiesocidae (clingfishes)						
Chorisochismus dentex (Pallas)	0,55	4,74	1,00	12,07	0,83	9,42
Eckloniaichthys scylliorhiniceps Smith	–	–	0,02	0,01	0,01	0,01
Gobiidae (gobies)						
Caffrogobius caffer (Günther)	1,44	12,23	0,14	0,40	0,61	4,68
Total number of fish	513,00		1028,00		1541,00	
Total biomass (g)	4020,51		6285,96		10306,47	
Pool area sampled (m^{-2})	75,22		132,60		207,82	
Pool area % shore area	8,05		9,91		9,12	
Number of fish (m^{-2} pool area)	6,82		7,75		7,42	
Biomass (m^{-2} pool area)	53,45		47,41		49,60	
Number of fish (m^{-2} shore area)	0,55		0,60		0,58	
Biomass (m^{-2} shore area)	4,30		3,20		3,67	

both coasts, their vertical distribution patterns are similar on the two coasts, although on the West Coast they usually extend slightly higher (about 30 cm) up the shore.

Three groups of species may be recognized according to the zones that they occupy on the shore. The first group occurs mainly at high levels, primarily from mean tide level (ML) upwards to the highest pools. Species of the second group are distributed throughout the intertidal zone, while the third group of species occupies lower levels, usually below mean low water of neap-tides (MLWN). This division of intertidal species into three groups is essentially the same as that described by other authors (see Gibson 1982).

Clinus acuminatus was the only species found exclusively high on the shore on both sides of the Peninsula. *Caffrogobius caffer* occurred only in high shore pools on the West Coast, but in False Bay it was distributed throughout the intertidal zone, although more abundant above ML. Two other species, *Clinus cottoides* and *C. superciliosus* occupied the whole shore in False Bay, the former being more abundant between MLWN and ML and the latter below MLWN. Four species were distributed throughout the intertidal zone on the West Coast, namely *Clinus superciliosus, C. heterodon, C. cottoides* and *C. dorsalis*. *Clinus heterodon* was captured only on the West Coast, where it was most abundant between MLWN and MHWN. *Clinus cottoides* was most abundant at similar levels as in False Bay, whereas *C. superciliosus* was abundant at all levels, not only low on the shore as on the False Bay coast. *Clinus dorsalis* occurred only below MHWN in False Bay. The remaining species, 12 in False Bay and seven on the West Coast, were group three species, occurring in greatest abundance below MLWN.

Superimposed on the zonation patterns described above are intraspecific differences in size distribution of different fish. Very small *Chorisochismus dentex* (<20 mm) were, for example, found only below MLWN, those of intermediate size (20–60 mm) occurred throughout the tidal range of the species but larger individuals (>100 mm) were again found only below MLWN. *Clinus superciliosus* of <75 mm occurred at all intertidal levels, but larger individuals (>110 mm) seldom occurred above ML. *Clinus cottoides* displayed a similar pattern, with individuals longer than 60 mm seldom occurring above MHWN. The reverse trend was shown by *Clinus acuminatus*, an upper shore species, and *C. heterodon*, a primarily mid-shore species; larger individuals of both these species occurring

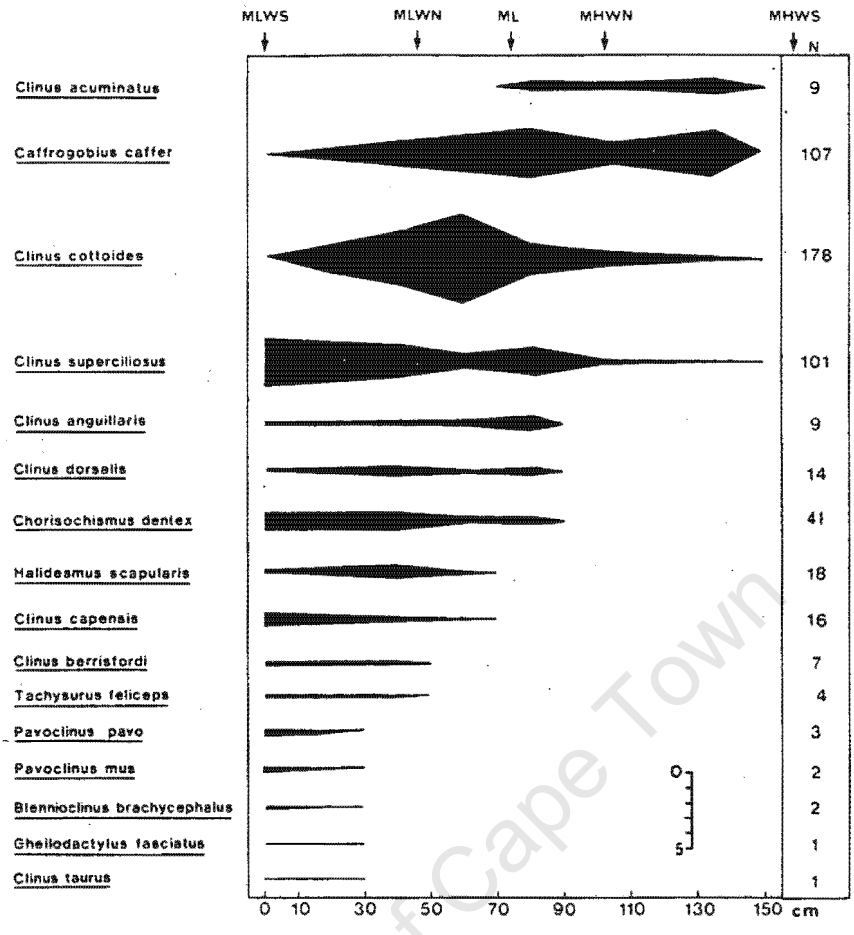

Figure 2 Zonation and abundance (m^{-2} pool area) of rock-pool fish species on the False Bay coast of the Cape Peninsula.

only near the upper distribution limits of the species.

Vertical zonation of rocky shore intertidal fish has been described by a number of other workers (see Gibson 1969, 1982). Although experimental work on factors imposing upper and lower distribution limits is limited, there is some evidence to suggest that they are similar to those influencing the distribution of intertidal invertebrates and algae (Gibson 1972). For a review of these factors, see Newell (1979).

There are two descriptive accounts of the vertical zonation patterns of intertidal fish on the south-western Cape coast of South Africa. Jackson (1950) provides a diagram showing heights on the shore at which 16 species may most frequently be found on the Cape Peninsula and Penrith (1965) provides information on the relative abundance of clinids in four vertical zones at 'typical' west and south coast localities. The abundance of the different species is quantified in this report but the zonation patterns are similar to those described previously.

One additional aspect of zonation evident from this study is that the vertical distribution of species on the more exposed West Coast is noticeably higher than that on the False Bay coast. This is contrary to Gibson's (1982) proposal that fish on rocky shores usually shift their distribution downwards in response to increased wave action. The upshore shift evident here may be a result of the larger waves flushing high-shore pools more often, thus reducing physical stress and increasing feeding time. This type of argument has often been used to explain the upshore shift of sessile invertebrates and algae (Newell 1979). The profiles of the localities sampled on the West Coast were also less steep than at the sites in False Bay. It is therefore possible that, even though the waves are larger on the West Coast, the less steep shore causes wave action to be attenuated at higher levels. Thus the direct effects of turbulence on West Coast fish may actually be less than indicated by offshore measurements of swell height.

Factors affecting abundance and diversity

Interpretation of the abundance and diversity patterns of the fish populations on the two coasts requires some comparisons of the physical characteristics of the pools sampled (Table 2).

The intertidal zone at the West Coast sites was on average wider (maximum 83 m) than that in False Bay (maximum 37 m), resulting in a difference in the mean distance of the pools from LWS. (The greater width of the intertidal zone is the main reason that more pools were sampled on the West Coast.) Average rock and algal cover and mean pool area were similar on both sides of the Peninsula, whereas mean height of the pools above LWS and mean pool volume were greater on the West Coast, although not significantly so ($P > 0{,}05$) owing to the large variances. The only physical parameter that did differ significantly ($P < 0{,}005$) was the maximum depths of the pools, pools on the West Coast being on average deeper.

Correlations between all possible pairs of environmental variables are shown in Table 3. The height of pools increased significantly with increasisng distance from LWS on the West Coast, but not in False Bay because, although intertidal topography was uneven on both coasts, the intertidal zone on the West Coast was wider, allowing greater resolution. Pool area, volume and depth were all significantly correlated with each other on both coasts but these cross correlations are not surprising considering the way in which volume was calculated.

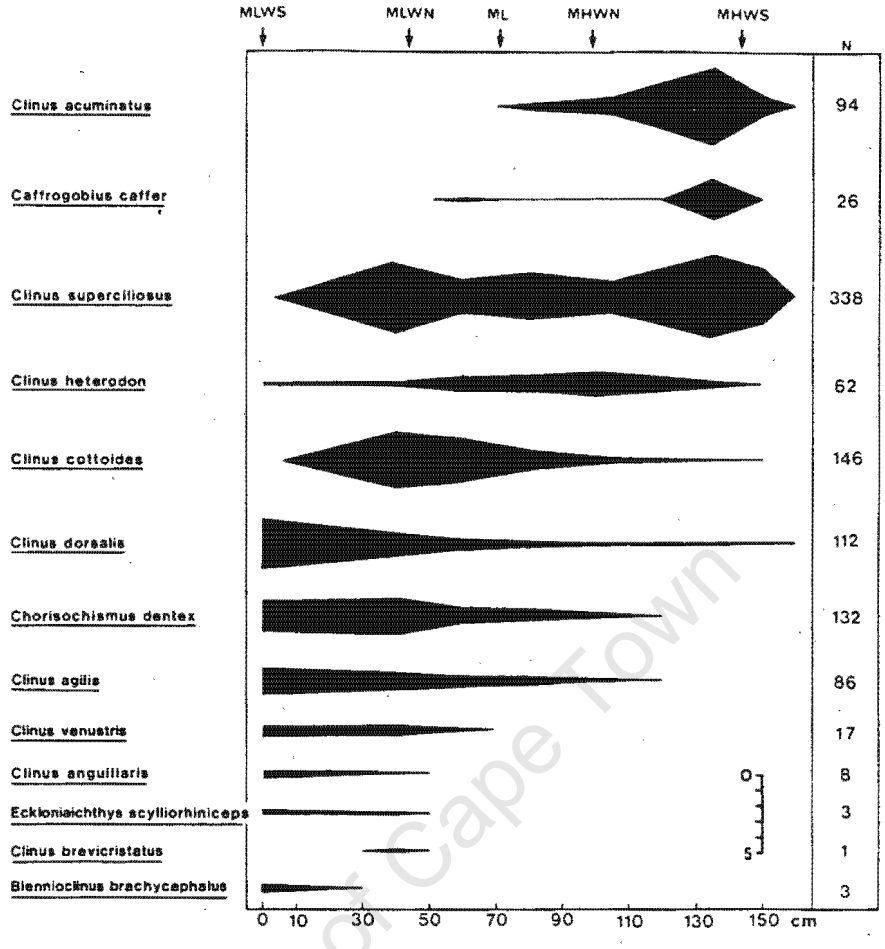

Figure 3 Zonation and abundance (m^{-2} pool area) of rock-pool fish species on the West Coast of the Cape Peninsula.

Table 2 Comparison of the physical characteristics of the rock pools that were sampled on the False Bay and western costs of the Cape Peninsula

	False Bay		West Coast		Significance
	Range	Mean	Range	Mean	($P < 0,01$)
Distance from LWS (m)	1,5 – 37,0	14,68	1,0 – 88,0	22,06	$P < 0,001$
Height above LWS (cm)	12 – 147	69,18	5 – 287	87,37	NS
Area (m^2)	0,13 – 11,13	2,82	0,17 – 12,40	2,60	NS
Volume (l)	7 – 2617	293,85	16 – 2240	467,41	NS
Maximum depth (cm)	9 – 75	22,50	7 – 67	31,30	$p < 0,005$
Rock cover	0 – 9	3,21	0 – 8	2,90	NS
Weed cover	0 – 9	2,82	0 – 8	2,96	NS

Table 3 Coefficients of correlation within the environmental variables of the pools sampled on the False Bay (FB) and western coasts (WC) of the Cape Peninsula (*$P < 0,01$)

	HGHT		DIST		AREA		VOL		MAXD		ROCK	
	FB	WC	FB	WC	FB	WC	FB	WC	FB	WC	FB	WC
DIST	0,27	0,50*										
AREA	−0,23	−0,12	0,38	0,33								
VOL	−0,39	−0,05	0,35	−0,01	0,83*	0,75*						
MAXD	−0,44	0,32	0,31	0,01	0,55*	0,36*	0,78*	0,47*				
ROCK	−0,36	−0,35	0,35	0,09	0,37*	0,36*	0,40	0,44*	0,28	0,09		
WEED	−0,22	−0,06	0,40	0,15	−0,27	0,08	−0,18	0,01	0,01	−0,19	−0,19	0,03

Two significant correlations that are of importance in later analysis are those between the two measurements of pool size (area and volume) and rock cover for the West Coast data.

Correlations between the fish community and aspects of the pool environment

On the False Bay coast, the number of species, total number of fish and biomass per pool all exhibited highly significant positive correlations ($P < 0{,}001$) with the amount of rock cover present in the pools (Table 4). Pool size, as measured by both surface area and volume, was also significantly correlated ($P < 0{,}01$) with these three dependent variables. Pool depth seemed to be somewhat less important, while height above LWS showed a significant negative correlation only with the number of species per pool. No correlation was apparent between any of the dependent variables and distance from LWS or the amount of algal cover present.

Very similar relationships between the dependent variables and environmental factors were evident on the West Coast (Table 4). Highly significant positive correlations ($P < 0{,}001$) were recorded between all three dependent variables and both rock cover and pool volume. The number of species and number of fish both showed significant positive correlations with area, but the correlation between this variable and biomass was not significant. Only the number of species per pool correlated (negatively) with height above LWS. No other correlations were significant.

Table 4 Correlation of number of species (SPNO), total biomass (MASS) and total number of fish (TOTNO) in rock pools sampled on the False Bay and west coasts of the Cape Peninsula with environmental variables measured in the pools (* denotes significance $P < 0{,}01$)

	SPNO		TOTNO		MASS	
	FB	WC	FB	WC	FB	WC
HGHT	−0,53*	−0,47*	−0,33	−0,26	−0,36	−0,20
DIST	−0,25	−0,26	−0,10	−0,03	−0,14	−0,17
AREA	0,53*	0,60*	0,65*	0,84*	0,63*	0,20
VOL	0,63*	0,45*	0,55*	0,75*	0,65*	0,50*
MAXD	0,51*	0,38	0,36	0,25	0,51*	0,23
ROCK	0,81*	0,55*	0,66*	0,57*	0,75*	0,51*
WEED	−0,27	0,06	−0,16	0,02	−0,21	−0,13

The results of the stepwise multiple regression analyses are shown in Table 5 (False Bay) and Table 6 (West Coast). In summary, at least 58% and up to 88% of the variance in the rock pool fish populations on both sides of the Peninsula can be explained by the environmental factors measured.

In the False Bay sites, variance in the number of species per pool is best explained by a linear model; the total number of fish per pool by a log-linear model and biomass is almost equally well explained by log-linear or log-log models. In each case, the relationship between the dependent variable and rock cover is positive and highly significant ($P < 0{,}001$) and accounts for between 65% and 76% of the variance. Measurements of pool size also contribute significantly ($P < 0{,}05$); volume explaining 11% of the variance in the number of species and 9% or 15% in biomass (depending on the model chosen), and area 19% in the number of fish per pool. The only other significant independent variable is height above LWS which

Table 5 Coefficients of determination for different models of stepwise multiple regression on the False Bay data. Dependent variables are SPNO, TOTNO and MASS and independent variables are environmental factors. Only those environmental factors contributing significantly ($P < 0{,}05$ *F*-test) to an explanation of the variance are included

Model	SPNO		TOTNO		MASS	
Lin – lin	ROCK	0,65	ROCK	0,44	ROCK	0,57
	VOL	0,11	AREA	0,19	VOL	0,15
	HGHT	0,03				
Log – lin	ROCK	0,55	ROCK	0,69	ROCK	0,70
	VOL	0,09	AREA	0,19	VOL	0,15
Lin – log	ROCK	0,56	VOL	0,44	VOL	0,52
	VOL	0,09			ROCK	0,08
	HGHT	0,06				
Log – log	ROCK	0,55	ROCK	0,70	ROCK	0,76
	VOL	0,67	VOL	0,11	VOL	0,09

explains 3% of the variance in the number of species inhabiting the pools.

Stepwise multiple regression analysis of the West Coast data shows somewhat different results (Table 6). In general, less of the total variance is explained by the environmental factors measured than was the case for the False Bay data. Nevertheless, between 58% and 80% of the variance in the fish populations can be accounted for. Linear models give the highest coefficients of determination for both the number of species and total number of individuals per pool, whereas the variance in biomass is best explained by a log-log model.

On the West Coast pool surface area is the environmental variable explaining the highest percentage of the variance in all three dependent variables, as opposed to rock cover in False Bay. Rock cover is of secondary importance, accounting for between 6% and 12%, height above LWS (16%) is significant only in an explanation of the variance in the number of species, and distance from LWS (4%) only in biomass.

In False Bay, rock cover is the critical variable controlling the fish community whereas on the West Coast, pool area is

Table 6 Coefficients of determination for different models of stepwise multiple regression on the West Coast data

Model	SPNO		TOTNO		MASS	
Lin – lin	AREA	0,36	AREA	0,71	ROCK	0,26
	HGHT	0,16	ROCK	0,08	VOL	0,09
	ROCK	0.06			AREA	0,07
Log – lin	ROCK	0,28	AREA	0,52	ROCK	0,47
	AREA	0,11	ROCK	0,16	AREA	0,14
	DIST	0,09				
Lin – log	AREA	0,32	AREA	0,51	ROCK	0,17
	HGHT	0,18	ROCK	0,04	DIST	0,09
Log – log	ROCK	0,27	AREA	0,59	AREA	0,49
	AREA	0,10	ROCK	0,07	ROCK	0,13
	DIST	0,08			DIST	0,04

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more important, posing the question as to why there should be a difference between the two coasts. Before attempting to answer this question, our results should be compared with those of two previous studies.

Marsh, Crowe & Siegfried (1978) reported total cover (a combined measure of rock and algal cover) to account for approximately 70% of the variance in the abundance of clinids per pool. Rock cover alone, as well as depth, were of secondary importance and no significant relationship with pool size was obtained. Their study was conducted at Bailey's Cottage, very close to one of our transect sites in False Bay. However, since they concentrated on small pools, formed mainly in crevices and depressions in solid bedrock, both pool size and the amount of rock cover were small and fairly uniform. All size and cover readings fell within a fairly narrow range and hence these two variables did not correlate significantly with the fish populations inhabiting the pools.

For the effects of pool size to be detected, it is essential that enough pools encompassing a wide range of physical factors, are analysed. The way in which rock cover is estimated is also important. If rock cover is calculated as a percentage of pool area, then small pools can have values as high as larger ones, although considerably less cover is available in absolute terms. This method of estimation was used by Marsh *et al.* (1978) and Gibson (1972), who analysed rock pool fish populations in exposed and sheltered areas on the coast of France. Gibson's multiple regression analyses showed that level and area are significant in accounting for variance in the number of fish in pools on sheltered shores, whereas cover (also rock and algae combined) was not significant. On exposed shores, none of the environmental factors that he measured were significant.

In this study, estimates of cover were based not on a relative but an absolute scale of amount of cover in the pools, such that very small pools could not have high cover ratings. For this reason, rock cover on the West Coast increased significantly with increasing pool size. The size distribution of False Bay pools was skewed to the left (i.e. a predominance of smaller pools was sampled), so that the size range of pools was inadequate to show a significant relationship between pool size and rock cover. To illustrate this point, it can be shown that if only those pools on the West Coast within the limited range of $2{,}0-3{,}2\ m^2$ ($N = 14$) are re-analysed, the abundance of fish present is significantly correlated ($P < 0{,}01$) with rock cover, but not with pool area or volume.

The amount of rock cover is the most important factor regulating the abundance of fish in rock pools around the Cape Peninsula whereas size is significant only because larger pools can incorporate more cover.

Reasons for the relationship between rock cover and abundance

Correlations alone cannot establish cause and effect relationships so more fundamental reasons should be sought for why the abundance of rock-pool fish is related to rock cover. All species collected were small, cryptic and with the exception of *Caffrogobius caffer*, carnivorous (Bennett *et al.* 1983). Some proportion of the populations of these species are resident in rock pools and, with the exception of *Pavoclinus mus, P. pavo, Clinus brevicristatus* and *Eckloniaichthys scylliorhiniceps* which are not found in rock pools devoid of algae (Penrith 1965; pers. obs.), spend most of the low tide period concealed in rocky cover. The few small individuals of *Clinus superciliosus* and *Caffrogobius caffer* which may be seen in the open rapidly take refuge when approached (Marsh *et al.* 1978; pers. obs.). Bennett *et al.* 1983 calculated that probably not enough food is available in the pools to sustain resident fish populations. A proportion of the food must therefore come from outside the pools. The importance of dislodged food washed into the pools during high tide relative to food actively sought by fish emigrating from the pools to forage over areas which are only covered at high tide is unknown. Some species, such as *Clinus superciliosus, C. cottoides* and *Chorisochismus dentex* leave pools at high tide. The guts of these species contain items which do not normally occur in pools, such as the cirri of barnacles.

Penrith (1965) and Marsh *et al.* (1978) observe that cover for fish is also cover for some of their prey species such as amphipods, isopods, molluscs and decapods. Thus fish remain in the same areas as their prey. The relative scarcity of fish in areas peripheral to cover, suggests however that fish gain other direct benefits from cover.

Morphological adaptations that enable intertidal fish to resist turbulence have been reviewed by Gibson (1969, 1982). Many of these adaptations are evident amongst the species examined here. Gibson also reviews work suggesting that fish largely avoid turbulence by remaining in holes and crevices amongst rocks. Observations on the reactions of South African species to turbulence are available only for *Caffrogobius caffer*. This species is probably the least 'cover dependent' examined in this study since, relative to their abundance, they were most frequently observed in the pools at low tide. Butler (1981) showed that this species took to cover when water flow reached a critical rate. Movement out of pools only occurred during early stages of the rising and late stages of the ebbing tide when water movement was below the critical rate. The fact that all the other species spend almost all their time under cover in pools at low tide when they are not subject to any turbulence, suggests that, at low tide at least, there are additional reasons for the high correlations with rock cover.

The most obvious direct benefit that can be gained from remaining under cover is protection from predators. The major predators on intertidal fish around the Cape Peninsula are probably birds, other fish and humans. Six of the species investigated in this study feed on other fish (Bennett *et al.* 1983); birds such as little egrets (*Egretta grazetta*), kelp gulls (*Larus dominicanus*) and cormorants (*Phalacocorax* spp.) forage in rock pools at low tide (Biden 1930; Skead 1966; pers. obs.); and children armed with hand-nets frequently pursued fish in rock pools in the study areas. The intensity of predation by birds and other fish on rock-pool species is unknown, but a low intensity of predation might be sufficient for cryptic behaviour to be advantageous in evolutionary terms.

Reasons for the relationships between rock cover, height and diversity

The number of species of fish recorded in each pool was significantly correlated with rock cover, pool size (≡ rock cover) and the height of the pools above LWS. Together, these three variables accounted for 58% and 85% of the variance in species diversity on the West Coast and in False Bay respectively. In their multiple regression analyses, Marsh *et al.* (1978) found only weed cover to be significant and Gibson (1972) showed that the number of species decreased with shore level, although apparently no attempt to correlate diversity with other environmental parameters was made.

Decreasing diversity up the shore has been documented by previous workers (see Gibson 1969, 1982 for review), and may occur because of the progressively more variable and extreme physical conditions in high shore pools (Newell 1979).

Gibson (1972) observes that where species overlap in ver-

tical distribution the microhabitats occupied by each are different and Critchlow (1972, in Gibson 1982) found that microhabitat specialization was greater where species diversity is high. In this study, three or more species were found in 54% of the pools sampled, six or more in 12%, while 10 species occurred in three pools. Some qualitive information concerning the habitat preferences of South African species is available (Jackson 1950; Penrith 1965; Butler 1981; Bennett *et al.* 1983), but it is not sufficiently detailed to resolve the manner in which the rock-pool habitat is subdivided. The rock-dwelling species, show substantial interspecific variation of body form (see Penrith 1969; Smith 1965 for illustrations and measurements) suggesting that they are morphologically adapted to using different microhabitats. If this is the case and it is assumed that more rock cover results in greater habitat diversity, then the correlation between species diversity and rock cover follows.

Marsh *et al.* (1978) found weed cover to be the only variable significantly correlated with species diversity. This is somewhat surprising since they caught no typically weed-dwelling species, over half their pools contained only one species, and the distribution of weed cover was heavily skewed to the left. For these reasons, their result may well be an artefact of sampling. It would only require a few of the pools containing more than one species to be low on the shore, to be larger or to have more rock cover, to enable weed cover to appear significantly correlated with species diversity.

Conclusions

Three lines of evidence support the hypothesis that physical characteristics of rock pools are critical factors limiting the abundance and diversity of intertidal fish communities in the south-western Cape. Firstly, there is no significant difference in the numbers of fish inhabiting similar pools between areas where the number of pools per unit shore area is different. The carrying capacity of the pools is therefore likely to be limited. Secondly, the population structure of the rock-pool fish is stable both seasonally and for longer periods, indicating that their numbers and diversity are limited by factors that remain constant. Finally, there is not enough food available in the pools to sustain the resident populations — some food must therefore be obtained outside the pools. Since none of the species are found intertidally other than in rock pools, it may be assusmed that the fish are 'concentrated' in the pools at low tide.

The amount of rock cover available was the most important of the environmental variables accounting for observed variance in the abundance and diversity of the fish populations. The importance of rock cover is attributed to the protection it provides from predators and wave turbulence. Increased rock cover may also increase the number of microhabitats available for different species. Microhabitat specialization can, however, only be inferred from the morphological diversity within this group of species, since no detailed observations of habitat preferences are available. Similarly, the relative importance of protection provided from predators and wave action cannot be evaluated since very little is known of predation pressure, high tide movements and the reaction of the species to waves during high tide.

Finally, Penrith (1970) found that after the pools are cleared of fish they remain unoccupied for at least six months before recolonization commences. Marsh *et al.* (1978) and Butler (1981) using mark-recapture techniques, also found that individual fish exhibit a high fidelity to particular pools. These last two points provide additional indirect evidence of the importance of rock cover. Recolonization is slow because of pool fidelity which may have evolved because of the necessity of regaining rock cover during tidal exposure.

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CHAPTER 2.

The diets of littoral fish from the Cape Peninsula

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Intertidal fish communities in the south-western Cape have a high density and biomass, implying that the fish are important consumers in the intertidal zone. Stomach content analyses of 20 species were undertaken to ascertain which food resources are most heavily exploited and the extent to which the co-existing fish compete for the same food resources. Three prey types, amphipods, isopods and polychaetes, occur in the diets of almost all the species examined and together comprise more than half the total volume consumed by 14 of the species. Despite the overlap in food types consumed, there was considerable subdivision of the resource, much of which may be explained in terms of horizontal and vertical distribution patterns of the various fish species, their habitat preferences, mouth sizes and changes in diet during growth. The standing stock of food in the pools is thought to be too low to support the resident fish populations, suggesting that some food, at least, is obtained outside the pools while the tide is in. For this reason, the fish are considered to be concentrated in the pools at low tide, indicating that the availability of suitable pool habitats may be important in controlling the densities of intertidal fish communities.

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Visbevolkings van die getysones van die suidwestelike Kaap het hoë digthede en biomassas, wat aandui dat die visse belangrike roofdiere van die sone is. Maaginhoudanalises van 20 spesies is onderneem om vas te stel watter voedselbronne die meeste benut word en die mate van kompetisie tussen simpatriese vissoorte vir dieselfde voedselsoorte. Drie prooi-kategorieë, nl. Amphipoda, Isopoda en Polychaeta kom voor in al die spesies wat ondersoek is en vorm saam meer as die helfte van die totale volume wat deur 14 spesies geëet is. Ten spyte van die oorvleueling van voedselkategorieë, was daar heelwat verdeling van die bron, wat grotendeels verklaar kan word deur die horisontale en vertikale verspreidingspatrone van die onderskeie visspesies se habitatvoorkeure, mondgroottes en verandering van dieet gedurende groei. Die gedagte bestaan dat die biomassa van die voedsel te laag is om die plaaslike visbevolking te onderhou, wat daarop dui dat ten minste 'n gedeelte van die voedsel ver buite die poele gedurende hooggety verkry word. Daar word dus aangeneem dat die visse gedurende laaggety in die poele gekonsentreer is, wat aandui dat die beskikbaarheid van geskikte poelhabitatte belangrik kan wees ten opsigte van die beheer van die digtheid van die visbevolkings van die getysones.

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Little information on the feeding ecology of South African littoral fish has been published. In 1945 Smith made the observation that clinids, the most abundant group, were carnivorous. Since then, data on the diets of eight species sampled from the intertidal zone have been published, all by people working in the eastern Cape. Christensen examined the dietes of *Clinus cottoides* (1978a), *Pavoclinus graminis* and *P. laurentii* (1978b), and three sparid species (1978c). Stobbs (1980) provided information on the feeding of *Chorisochismus dentex* and Butler (1982) attempted to relate the feeding of *Caffrogobius caffer* with the tidal cycle and time of day.

Despite the paucity of published works, a considerable body of unpublished information is available on the feeding ecology of intertidal fishes, particularly in the south-western Cape. Penrith's (1965) doctoral thesis includes a detailed analysis of the diets of six common clinid species and notes on several others; Pitt-Kennedy (1964), in an honours project, examined the diets of the two most abundant gobiid species; Jackson (1950) in his unpublished M.Sc. thesis, provides brief notes on the diets of six clinid species, a goby and *Chorisochismus dentex*; Hutchings (1968) described the diet of the sparid *Sarpa salpa*; and Branch (unpublished) has accumulated a considerable amount of fish feeding data during his extensive studies of intertidal communities.

Further information has recently been collected by Bennett & Griffiths (unpubl.) in the course of an analysis of distribution patterns of littoral fish on the Cape Peninsula. For the purposes of the present analysis data from these sources have been pooled to give an overall sample of 1 938 stomachs from twenty different species representing six genera. The data of Hutchings (1968) are not included as *Sarpa salpa* is not usually resident in the intertidal zone and those of Jackson (1950) were presented in insufficient detail to be included in the analysis.

It is hoped that this comparative information will help to indicate which food items are most heavily exploited by littoral fish communities as a whole and show to what extent co-existing species may compete for the same food resources.

Material and Methods

A list of fish species treated in this study, and of the sources of all material referred to, is given in Table 1. The fish were collected at low tide from intertidal rock pools and gulleys, mainly by poisoning with rotenone dissolved in acetone, but hand nets and baited hooks were also used on occasion. All fish were killed by placing in formalin or alcohol, after which they were transferred to formalin for storage.

Only the stomach contents were analysed, food elsewhere

Table 1 Sources of the data on which this study is based

Species	Number of guts examined				
	M.L. Penrith (1965 unpubl.)	G.M. Branch (unpubl.)	S. Pitt-Kennedy (1964 unpubl.)	Present study	Totals
Clinidae					
Clinus acuminatus	30	32		3	65
C. agilis	106			3	109
C. anguillaris		2		15	17
C. berrisfordi				7	7
C. brevicristatus	7				7
C. capensis	8	5		14	27
C. cottoides	169	178		19	366
C. dorsalis	25	18		12	55
C. heterodon	9			50	59
C. superciliosus	312	313		20	645
C. taurus				3	3
C. venustris				18	18
Pavoclinus graminis	9				9
P. mus	109				109
P. pavo	7	2			9
Blennioclinus brachycephalus	47			4	51
Gobiidae					
Caffrogobius caffer		162	96		258
C. nudiceps		5	41	9	55
Gobiesocidae					
Chorisochismus dentex				50	50
Congrogadidae					
Halidesmus scapularis				19	19

in the digestive tract was usually in an advanced stage of digestion and its inclusion in analyses would have prejudiced results in favour of less digestible food items. Sample sizes for each species (Tables 1 and 2) reflect only the number of stomachs examined that actually contained food. Unless otherwise stated, all fish length measurements are standard length (SL).

The stomachs were opened into water in a watch glass or petri-dish under a dissecting microscope and all contents removed. Food items were identified to species wherever possible and then grouped into higher taxa, usually orders. The displacement volume of each category was then measured in 25 or 10-ml measuring cylinders. Where volumes were small (<0,1 ml), volumes were estimated with the aid of an eyepiece micrometer or a 1,0-mm^2 grid placed under the petri-dish.

Several methods have been devised for assessing the relative importance of different food organisms in the diets of fishes. Most of these methods can be criticized on various grounds (see Hynes 1950, Berg 1979). For the purposes of the present study, the volumetric and frequency of occurrence methods were used. Volumes of each prey category are expressed as a percentage of the total volume consumed by each fish species and occurrence is the proportion of stomachs containing a particular food category, expressed as a percentage of total number of stomachs examined.

Results

Twenty species of fish were recovered in sufficient numbers to permit a meaningful analysis of stomach contents. The most abundant group were the Clinidae (klipfishes) with sixteen species (12 *Clinus*, 3 *Pavoclinus* and 1 *Blennioclinus*), which together made up over 70% of the fish caught. The remaining fish consisted of Gobiidae (gobies) with two species, of which one (*Caffrogobius caffer*) was very common, one species of sucker fish *Chorisochismus dentex* (family Gobiesocidae) and the eel-like *Halidesmus scapularis* (Congrogadidae).

The numbers of each species of fish examined, their size ranges and the composition of the stomach contents, by volume and percentage occurrence, are given in Table 2. The percentage occurrence of individual prey species in the stomachs of each fish is shown in Table 3. The feeding habits and diets of each species of fish analysed are discussed individually below.

(1) *Clinus acuminatus* was recorded almost exclusively near the top of the shore in barren rocky pools. It occurs on both the west and south-west coasts but is more abundant west of Cape Point. This species seldom attains more than 120 mm (Penrith 1965).

Sixty-five specimens between 34 mm and 127 mm were found to have food in their stomachs. Decapods (32%), molluscs (19%) and goose barnacles (15%) were the most important food items by volume, although all three categories occurred infrequently. The most frequently occurring food categories were amphipods (62%), isopods (53%) and polychaetes (16%).

Clinus acuminatus changes its diet with increasing size. Fish less than 50 mm rely almost exclusively on amphipods, isopods and polychaetes, while for individuals longer than 80 mm decapods and molluscs are of primary importance, although the other taxa continue to be taken.

No prey species had a particularly high frequency of occurrence in the sample examined (Table 3). Eight species occurred in more than 5% of the fish examined, the amphipods *Paramoera capensis* (12%) and *Hyale* spp. (11%) occurring most often. The occurrence of goose barnacles in the stomachs indicates that *C. acuminatus* will feed opportunistically on any suitable food that becomes available.

(2) *Clinus agilis* is abundant on the west coast, but becomes considerably less common east of Cape Point. This species inhabits weedy pools in the middle and lower areas of the intertidal zone. The species is small, seldom exceeding 100 mm (Penrith 1965).

The stomachs of 109 specimens ranging between 32 mm and 95 mm were examined. In comparison with other clinids, *C. agilis* has a restricted diet, prey from only three categories being consumed in appreciable amounts. Amphipods were the most important constituent with 44% by volume and 84% occurrence. Isopods (23% volume, 46% occurrence) and polychaetes (26% and 34%) were next in importance. Other items such as small gastropods, tanaids and copepods occurred in up to 10% of the stomachs, but did not contribute significantly to volume.

Nine prey species occurred in more than 5% of the fish examined, the more important species were the amphipod *Paramoera capensis*, which occurred in 58% of the fish examined, the isopod *Ianiropsis palpalis* (21%) and the polychaete *Platynereis dumerilii* (25%).

There are no pronounced changes in, or additions to, the diet of this species with increasing size.

(3) *Clinus aguillaris* is an elongate species occurring along both the western and southern Cape coasts at all but the-

Table 2 The diets of 20 littoral fish species in the south-western Cape (– indicates <0,5% contribution to volume)

					Food category																									
	Number of	Length range		Mouth size	Amphipods		Isopods		Polychaetes		Tanaids		Molluscs		Copepods		Ostracods		Insects		Decapods		Barnacles		Fish		Algae		Echinoderms		Other	
Species	stomachs	min.	max.	(% SL)	%occ.	%vol.	%occ.	%vol.	%occ.	%vol.	%occ.	%vol.	%occ.	%vol.	%occ.	%vol.	%occ.	%vol.	%occ.	%vol.	%occ.	%vol.	%occ.	%vol.	%occ.	%vol.	%occ.	%vol.	%occ.	%vol.	%occ.	%vol.
Clinus acuminatus	65	34	127	12	62	10	53	12	16	7	5	–	5	19	8	–			5	1	11	32	3	15	6	1					11	3
C. agilis	109	32	95	11	84	44	46	23	34	26	9	4	10	–	9	–			1	–	1	–									7	2
C. anguillaris	17	59	186	8	82	18	53	30	6	12			41	2	12	–	6	–			29	38										
C. berrisfordi	7	63	109	12	14	7	71	23	14	1											57	26	86	43								
C. brevicristatus	7	50	61	11	71	50	14				14		28		14																	
C. capensis	27	56	121	11	100	79	11	9	11	7					7	–					7	3							4	–	11	2
C. cottoides	366	33	122	13	65	24	67	30	26	12	4	–	19	2			3	–	2	1	9	14	34	10	2	4					8	3
C. dorsalis	55	36	70	9	82	52	33	24	8	16					2	–			9	2	2	–									16	6
C. heterodon	59	32	108	12	28	21	28	28	22	22	6	2	10	3	8	3			14	15			10	5			2	1				
C. superciliosus	645	25	262	11	82	21	50	9	19	7	10	–	19	18	34	–	18	–	9	–	9	21	3	–	2	8	1	–	1	–	24	16
C. taurus	3	78	231	12	100	75	67	5	67	5			100	5							33	15										
C. venustris	18	32	69	10	73	25	60	20	7	–	7	2	27	2	33	3	13	–			7	9							53	34	13	5
Pavoclinus graminis	9	83	111	8	89	52	11						11		33						22											
P. nus	109	30	96	7	97	48	22	23	9	4			23	6	45	4	11	–			2	14										
P. pavo	9	42	84	8	100		33		11				11																			
Blennioclinus brachycephalus	51	30	92	8	92	51	60	17	26	18	43	12	6	–	9	–	10	–	17	–												
Caffrogobius caffer	258	27	133	11	23	1	19	3	11	1	4	–	19	29	23	–	13	–	9	1	2	3			4	–	51	60				
C. nudiceps	55	35	100	–	41	4	53	73	7	7	6	–	6	11	44	3	16	2	2	–					4	1					12	2
Chorisochismus dentex	50	15	225	16	86	10	86	11	38	6			76	52	4	–	6	–	8	–			10	4			10	8			14	9
Halidesmus scapularis	19	63	145	5	89	52	57	21			31	6	4	–			12	3	4	–							6	1			31	17

Table 3 Percentage occurrence of the prey species most frequently consumed by littoral fish in the south-western Cape. Only those species which occurred in five or more percent of stomachs are considered

	C. acuminatus	*C. agilis*	*C. anguillaris*	*C. berrisfordi*	*C. brevicristatus*	*C. capensis*	*C. cottoides*	*C. dorsalis*	*C. heterodon*	*C. superciliosus*	*C. taurus*	*C. venustris*	*P. graminis*	*P. mus*	*P. pavo*	*B. brachycephalus*	*C. caffer*	*C. nudiceps*	*C. dentex*	*H. scapularis*
Amphiphoda																				
Ampithoe sp.	–	–	6	–	–	–	–	–	–	–	–	–	11	–	–	30	–	–	–	–
Aora typica	–	–	6	–	–	–	–	–	–	–	–	–	–	–	–	19	–	–	–	–
Caprella scaura	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	23	–	–	–	–
Ceradocus rubromaculatus	–	–	–	–	–	16	–	–	–	–	33	6	11	–	–	–	–	–	–	–
Gitanopsis pusilla	–	–	–	–	14	–	–	–	–	–	–	–	22	–	–	13	–	–	–	–
Hyale sp.	11	9	18	–	14	16	5	10	22	11	33	11	33	19	22	–	5	–	30	11
Ischyrocerus anguipes	–	5	–	–	43	–	–	–	–	7	–	–	11	75	11	–	–	5	–	–
Jassa falcata	–	6	–	–	–	–	–	–	–	–	–	6	–	–	–	13	–	–	–	–
Lembos sp.	–	–	–	–	–	–	–	–	–	–	–	–	11	–	–	13	–	30	–	–
Lysianassa ceratina	–	6	–	–	–	–	–	–	–	7	–	6	–	–	–	13	–	–	–	–
Maera sp.	–	5	–	–	–	–	–	–	–	–	–	–	11	–	–	–	–	–	–	–
Melita sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	22	–	–	–	–	–
Paramoera capensis	12	58	29	–	14	58	18	20	8	38	100	28	56	24	89	–	–	13	12	21
Podocerus africanus	–	–	–	–	43	–	–	–	–	–	–	–	–	19	–	6	–	–	–	–
P. cristatus	–	–	–	–	–	–	–	–	–	–	–	–	11	–	–	9	–	–	–	–
Probaloides rotunda	–	–	–	–	–	26	–	–	–	–	–	11	–	–	–	–	–	–	–	32
Temnophlias capensis	–	–	–	–	14	–	–	–	–	–	–	–	–	–	–	9	–	–	–	–
Isopoda																				
Cymodocella sp.	–	–	–	–	–	–	5	–	8	–	–	–	–	–	–	–	–	–	–	–
Dynamenella huttoni	–	–	–	–	–	–	6	–	12	–	–	6	–	–	–	–	–	–	–	–
Exosphaeroma sp.	5	6	18	14	–	–	5	5	6	5	33	11	–	–	22	–	12	36	40	11
E. truncatitelson	8	6	–	–	14	–	8	–	–	–	–	6	–	–	–	–	6	15	8	–
Gnathia sp.	–	–	–	14	–	–	–	–	–	–	–	–	–	–	–	–	–	5	6	–
Jaeropsis curvicornis	–	–	–	–	–	–	–	–	–	–	33	–	–	–	22	23	–	–	–	–
Ianiropsis palpalis	5	21	12	14	–	–	5	8	–	13	–	–	11	–	–	42	5	–	6	–
Notacellus capensis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	21
Paridotea ungulata	–	7	–	–	–	–	–	–	–	5	–	–	–	12	–	–	–	–	–	–
Parisocladus perforatus	–	–	–	–	–	–	5	–	6	–	33	–	–	–	–	–	–	–	10	–
P. stimpsoni	6	–	–	–	–	–	9	–	–	–	–	–	–	–	–	–	–	–	10	–
Stenetrium bartholomei	–	–	–	–	–	5	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Insecta																				
Telmatogeton minor (larvae)	5	–	–	–	–	–	–	8	12	9	–	–	–	–	–	17	9	–	14	–
Tanaidacea																				
Anatanais gracilis	–	8	–	–	14	–	–	–	–	–	–	–	–	–	–	40	–	–	–	–
Leptochelia barnadi	–	–	–	–	–	–	5	–	–	9	–	–	–	–	–	–	–	5	–	11
Polychaeta																				
Gunnarea capensis	–	–	–	–	–	–	–	–	–	–	67	–	–	–	–	13	–	–	38	–
Platynereis dumerilii	–	25	–	–	–	–	9	–	12	7	–	–	–	–	–	9	–	–	–	–
Pomatoleios kraussii	–	–	–	–	–	–	8	–	–	–	–	–	–	–	–	–	–	–	–	–
Mollusca																				
Aetoniella nigra	–	8	–	–	29	–	9	–	8	12	67	–	11	5	11	6	–	–	–	–
Fissurella sp.	–	–	6	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	8	–
Gibbula rosea	–	–	6	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Helcion pectunculus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	10	–
H. pruinosis	–	–	12	–	–	–	–	–	10	–	–	–	–	–	–	–	–	–	18	–
Marginella capensis	–	–	18	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Oxystele spp.	–	–	6	–	–	–	6	–	6	–	–	–	–	–	–	–	12	–	6	–
Patella barbara	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	25	–
P. granatina	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	10	–
P. granularis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	16	–
Siphonaria sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	12	–
Tricolia sp.	–	–	–	–	–	–	–	–	–	–	67	–	–	11	–	–	–	–	–	–

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Table 3 (continued)

	C. acuminatus	*C. agilis*	*C. anguillaris*	*C. berrisfordi*	*C. brevicristatus*	*C. capensis*	*C. cottoides*	*C. dorsalis*	*C. heterodon*	*C. superciliosus*	*C. taurus*	*C. venustris*	*P. graminis*	*P. nus*	*P. pavo*	*B. brachycephalus*	*C. coffer*	*C. nudiceps*	*C. denitex*	*H. scapularis*
Pycnogonida																				
Tanystylum brevipes	–	–	–	–	29	–	–	–	–	–	–	–	11	–	–	–	–	–	–	–
Ophiuroidea	–	–	–	–	–	–	–	–	–	–	–	53	–	–	–	–	–	–	–	5
Decapoda																				
Cyclograpsus sp.	–	–	6	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Plagusia chabrus	5	–	24	43	–	5	7	–	–	–	33	6	22	–	–	–	–	–	–	–
Copepoda																				
Harpacticoidea	–	8	6	–	14	–	–	–	8	–	–	22	33	43	9	–	5	30	–	–

highest intertidal levels. Larger individuals are found lower on the shore than juveniles. The largest recorded specimen is 278 mm (Penrith 1969).

Seventeen specimens between 59 mm and 186 mm long were examined. Amphipods (82%), mainly *Paramoera capensis* and *Hyale* spp., and isopods (53%), mainly *Ianiropsis palpalis* and *Exosphaeroma* spp. occurred most frequently and provided 18% and 30% of the volume respectively. Decapods, mainly *Plagusia chabrus*, were the single most important food category, providing 38% of the volume consumed and occurring in 29% of the stomachs examined. Small molluscs occurred in 41% of the stomachs, but provided very little volume, the two most common species being *Marginella capensis* and *Helcion pruinosus*.

Although sample size was small there was definite evidence that diet changed with size. Small prey items such as amphipods, isopods and polychaetes were important to smaller individuals, whereas decapods and, to a lesser extent, molluscs became important in larger fish.

(4) *Clinus berrisfordi* is a little-known south-coast species. It occurs in rocky pools at the bottom of the intertidal zone. The largest recorded specimen is 109 mm long.

The seven specimens examined, ranging between 63 mm and 109 mm, all contained food. Barnacle cirri occurred in six of the individuals and constituted 43% of the total stomach content volume. The other apparently important food categories were decapods (*Plagusia chabrus*), which occurred in four of the specimens (26% by volume) and the isopods *Exosphaeroma* spp., *Gnathia* spp. and *Ianiropsis palpalis*, which occurred in five of the fish, making up 23% of the volume.

(5) *Clinus brevicristatus*. This is a rare species found in weedy pools in the lower intertidal zone from False Bay westwards. It seldom attains more than 100 mm in length (Penrith 1965).

The seven specimens examined ranged between 50 mm and 61 mm long. Amphipods were the only important diet category, occurring in five of the stomachs and accounting for half the volume. Eleven prey species were identified in the stomach contents, *Ischyrocerus anguipes* and *Podocerus africanus* being the most frequently occurring. Five other categories were present, each only represented by one identified species.

(6) *Clinus capensis* is a moderately elongate species with an acutely pointed snout and is the only species recorded here that bears barbels on its chin and snout. It is common in rocky pools low on the shore and subtidally from False Bay eastwards, but rare along the west coast, and attains 246 mm (Penrith 1969).

Twenty-seven specimens between 56 mm and 121 mm in length had food in their stomachs. Every individual contained amphipods which made up 79% of the volume consumed. Isopods and polychaetes were found in three fish and constituted nine and seven percent of the total volume respectively.

Four amphipod species and one isopod were identified. *Paramoera capensis* was found in 58% of stomachs, *Probaloides rotunda* in 26%, *Ceradocus rubromaculatus* and *Hyale* spp. in 16%. The isopod was *Stenetrium bartholomei*.

Decapod larvae, which were considerably larger than all the other prey items consumed by *C. capensis*, were found in two individuals of moderate size. There is, however, no evidence to suggest that a change in diet occurs with increasing size, since the major food of all species was small items even though mouth size of small individuals would have allowed the consumption of larger prey species.

(7) *Clinus cottoides* was the most abundant intertidal species from Cape Point eastwards. It is also very abundant on the west coast, though ranking second to *C. superciliosus*. *Clinus cottoides* occurs at all levels of the shore, but is most common in rocky pools at mid-tide levels. It is a smaller species than *C. superciliosus*, specimens over 115 mm being unusual (Penrith 1965).

A total of 366 guts from individuals ranging between 33 and 122 mm in length were analysed. Volumetrically isopods (30%) and amphipods (24%) were the most important food categories, but decapods (14%), polychaetes (12%) and barnacle cirri (10%) were also important. The most frequently occurring categories were isopods (67%), amphipods (65%) and barnacle cirri (34%).

Christensen (1978a) examined the stomachs of 82 *C. cottoides* from the eastern Cape, and the results of this study are similar to those presented here, although in his sample, isopods and polychaetes occurred more frequently and barnacle cirri less frequently.

Small *C. cottoides* feed mainly on amphipods and isopods, but when over 50 mm long a wider range of food items become important. Barnacle cirri occur most frequently in fish between 50 mm and 70 mm, decapods and polychaetes being most important in fish more than 80 mm long.

Seventeen prey species occurred in 5% or more of the guts examined. The barnacle cirri were mainly those of *Tetraclita serrata* and *Octomeris angulosa*, but cirri from other species were also taken. The only other species to occur in more than 10% of stomachs was the amphipod *Paramoera capensis*.

(8) *Clinus dorsalis* is a small elongate species seldom exceeding 70 mm (Penrith 1965). Common on both the western and southern Cape coasts, it is found at all except the very highest intertidal levels.

The stomach contents of 55 specimens ranging between 36 mm and 70 mm were analysed. The most important food category was amphipods which occurred in 82% of the sample constituting 52% of the total volume. Isopods were the second most important group, occurring in 33% of stomachs, and providing 24% of the volume. The only other major food category was polychaetes with 16% volume and 8% occurrence.

Five prey species occurred in 75% of stomachs examined, with *Paramoera capensis* and *Hyale* spp. being the most commonly consumed amphipods, and *Exosphaeroma* spp. and *Ianiropsis palpalis* the important isopods. The larvae of *Telmatogeton minor* occurred in 8% of stomachs.

There was no evidence for a shift in diet composition with increasing size.

(9) *Clinus heterodon* is common on the west coast but very rare in False Bay. It occurs in rocky and weedy pools mainly in the mid- and lower intertidal zone.

Fifty-nine specimens between 32 and 108 mm long were examined. Amphipods, isopods and polychaetes each provided approximately a quarter of the volume consumed and occurred in between 22% and 28% of the fish. Contributions of lesser importance were made by barnacle cirri and insect larvae. Important prey species were *Hyale* spp. and *Dynamenella huttoni* and *Telmatogeton minor*.

Changes in diet with size were apparent. Copepods and tanaids were taken only by fish less than 55 mm long. Isopods became less important with increasing size, although they did occur throughout the size range. Gastropods and chironomid larvae were relatively more important in fish over 80 mm long. The above trends should be treated with some caution since they may represent local food availability, the larger fish analysed all being captured in one area.

(10) *Clinus superciliosus* was the largest and most abundant species examined. It occurs at all intertidal levels and subtidally. Size segregation is apparent with smaller individuals predominating at higher intertidal levels.

A total of 645 stomachs from fish ranging between 25 and 262 mm were analysed. Volumetrically the most important food categories were amphipods (21%), decapods (21%), and molluscs (18%). In terms of occurrence amphipods (82%), isopods (50%) and copepods (34%), dominated the samples.

Changes in the relative importance of the different food categories did occur, larger food items becoming more important in the diets of larger fish. Amphipods, isopods, copepods and polychaetes became less important with increasing size whereas molluscs, decapods and fish are rarely taken by *C. superciliosus* less than 60 mm long and become increasingly more important in the diets of larger individuals.

One hundred and twenty two prey species were identified in the stomachs of *C. superciliosus*, with 11 species occurring in more than 5% of the sample. *Paramoera capensis* (38%) and *Hyale* spp. (11%) are the most commonly occurring amphipods, the isopod *Ianiropsis palpalis* was found in 13%, and the gastropod *Aetoniella nigra* in 12% of the stomachs examined.

(11) *Clinus taurus*. This is a rare species occurring at the bottom of the intertidal zone and subtidally around the entire Cape coast.

Three specimens, 78, 140 and 231 mm were examined and all had food in their stomachs. *Paramoera capensis* occurred in all stomachs and together with two other amphipod species, constituted 75% of the volume. Small molluscs also occurred in all three stomachs, but supplied only 5% of volume. A single crab, *Plagusia chabrus*, made up 15% of the volume.

(12) *Clinus venustris* occurs on the west and south coasts, but is rare east of Cape Point. A small species, it seldom exceeds 110 mm and is found only in low and mid-shore pools (Penrith 1965).

The stomachs of 18 individuals between 32 and 69 mm in length were analysed. Volumetrically the most important food was ophiuroids (34%) which occurred in 53% of stomachs. Six amphipod species, the most common being *Paramoera capensis*, occurred in 73% of the stomachs supplying a quarter of the volume, and isopods, mainly *Exosphaeroma* spp., occurred in 60% of the sample, providing 24% of the volume consumed.

The smallest individuals of this species contained only amphipods, isopods and copepods; whereas in those over 40 mm ophiuroids became important. The largest individual contained a decapod larva.

(13) *Pavoclinus graminis*. Known from False Bay eastwards, found in weedy pools and weedbeds in the lower intertidal zone. Attains approximately 140 mm (Penrith 1965).

The stomachs of nine specimens between 83 mm and 111 mm long were analysed. Amphipods formed 52% of the food volume and occurred in eight of the nine fish. A wide variety of prey species were taken (Table 3), with *Paramoera capensis* and *Hyale* spp. occurring most frequently. Two megalopae of *Plagusia chabrus* were present in the two largest fish and contributed considerably to the stomach contents volume. Christensen (1978b) examined the guts of 66 specimens collected in the eastern Cape and he also found amphipods to be the major food category.

(14) *Pavoclinus mus*. This was the only member of this weed-dwelling genus which was obtained in sufficient numbers to be used for a detailed study of feeding. It is one of the more highly modified weed-dwellers and is always taken amongst algae. *Pavoclinus mus* is a small species, not attaining more than 100 mm (Penrith 1965). It has not been found on the west coast.

Stomachs of 109 specimens between 30 and 96 mm were analysed. Amphipods were the most important food category, occurring in almost all the specimens examined and constituting approximately half of the total volume

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of food taken. Isopods were fairly important both in terms of volume (23%) and occurrence (22%). Copepods occurred in a high percentage of fish, but even a large number of harpacticoid copepods occupy only a very small volume.

Polychaetes were not found in fish smaller than 50 mm and their consumption increased in fish over this size. Isopods and molluscs, although present in small fish, become increasingly important in larger individuals. Copepods showed the reverse trend, occurring more frequently in smaller fish. Amphipods had a consistently high occurrence, but their contribution to volume decreased with increasing fish size.

Ten prey species were identified as having occurred in more than 5% of the *P. mus* stomachs examined. The tube-dwelling amphipod *Ischyrocerus anguipes* was by far the most commonly occurring species, being present in 75% of stomachs. Other amphipods, *Paramoera capensis, Podocerus africanus* and *Hyale* spp. were also frequently taken.

(15) *Pavoclinus pavo* occurs in weedy low-shore pools on the west and south coasts, but is nowhere very common. It is a relatively small species rarely reaching 110 mm in length (Penrith 1965).

Nine specimens, 42 mm to 84 mm, were examined. Amphipods formed the dominant food category in all the stomachs. *Paramoera capensis* occurred in eight of the specimens; *Ischyrocerus anguipes, Hyale* spp. and *Melita subchaelata* were also recorded. Small individuals of *Exosphaeroma* sp. and *Jaeropsis curvicornis* and the minute gastropod *Aetoniella nigra* were also recorded in one or more stomachs.

(16) *Blennioclinus brachycephalus* is locally common in low-shore pools east of Cape Point and less common along the west coast, where it is found only in sheltered areas. It is a small species apparently not attaining more than 100 mm (Penrith 1965).

Fifty-one stomachs from fish ranging between 30 and 92 mm in length were examined. Amphipods were the most important food category by both occurrence (92%) and volume (51%). Polychaetes occupied a relatively large volume (18%) and occurred in 26% of the sample. Isopods and tanaids occurred frequently (60% and 43% respectively), but occupied only small volumes.

Eighteen food species occurred in more than 5% of the stomachs examined. The amphipods *Caprella scaura, Aora typica* and *Ampithoe* spp. occurred in more than 20%, as did the isopods *Ianiropsis palpalis* and *Jaeropsis curvicornis* and the tanaid *Anatanais gracilis*.

Changes in diet composition with growth in this species appear to be negligible, no new categories or species becoming important as the fish increase in size.

(17) *Caffrogobius caffer* is the dominant species in barren high-shore pools east of Cape Point. It becomes progressively less abundant down the shore.

The stomachs of 258 fish between 27 and 133 mm long were examined. In terms of both volume and occurrence algae were the most important food category, comprising 61% and 51% respectively. *Ulva* spp. were the main algal species consumed but *Enteromorpha* sp., *Sargassum* sp. and *Cladophora* sp. were also taken. The only other important food category was molluscs (29% volume and 19% occurrence), *Oxystele* sp. being the most commonly consumed species. Amphipods (23%), isopods (19%), copepods (23%) and polychaetes (11%) all occurred frequently but, relative to the algae, their volume was very small.

Caffrogobius caffer exhibits a change in diet with size, small specimens being predominantly carnivorous whereas larger individuals are omnivorous, consuming large amounts of algae. The change-over occurs between 50 and 70 mm.

This species does appear to gain nutritional benefit from the algae it consumes, for Hamerton (1982) has shown that the energy content of faecal algae is lower than that ingested and, in addition, demonstrated destruction of the algal cells during passage through the gut.

(18) *Caffrogobius nudiceps* occurs in high amd midshore pools both east and west of Cape Point, but is more abundant on the west coast.

The stomachs of 55 specimens between 35 and 100 mm were analysed. This species was found to be entirely carnivorous with isopods of the genus *Exosphaeroma* dominating the diet (73% volume and 53% occurrence). Amphipods (41%), copepods (44%) and ostracods (16%) occurred frequently but together comprised only 9% of the volume.

There is some evidence of a change of diet with size, larger individuals taking larger food items such as fish and chitons, but the smaller prey categories continued to be important throughout the size range.

(19) *Chorisochismus dentex* is a relatively large species abundant on both the east and west coasts in rock pools from midshore downwards. Large individuals occur only near the low-water mark and subtidally. The species attains a total length of at least 300 mm (Smith 1965) and has a relatively very large mouth. It is the only species among those studied with large, strong incisors.

Fifty specimens 15 – 225 mm were examined. Amphipods and isopods occurred in 86% of the sample, but each made up only 10% of the volume of food consumed. The most important food category was molluscs, mainly limpets, which occurred in 76% of the stomachs examined and provided half of the volume. Polychaetes, sea urchins, chitons and barnacle cirri occurred in varying numbers of stomachs and provided between 4% and 8% of the volume.

Marked size-related trends in feeding were observed. Fish less than 25 mm long consumed only small crustaceans, mainly amphipods and isopods, although ostracods and copepods were important in the smallest fish. Crustaceans continued to be taken in decreasing amounts up to 150 mm after which they were virtually absent from the diet. Molluscs became increasingly important with fish size, occurring in all fish more than 180 mm long. Sea urchins occurred in a few of the largest fish. The heads of *Gunnarea capensis* and barnacle cirri were frequently taken by fish of intermediate size, being absent in all individuals less than 30 mm and more than 160 mm long.

The diet of *C. dentex* has previously been studied by Stobbs (1980) who examined 55 individuals from the eastern Cape. His findings concerning the relative contributions of the different food categories and changes in diet with size are very similar to those described above.

(20) *Halidesmus scapularis* is a small eel-like species, locally common in the lowest intertidal pools east of Cape Point. It attains a total length of approximately 175 mm (Smith 1965).

Nineteen specimens between 63 and 145 mm contained food. Eighty-nine percent of the fish examined contained amphipods, which constituted 52% of the total volume consumed. Isopods occurred in 57% of stomachs providing 21% of the volume. Tanaids and leptostracans occurred frequently, but did not contribute substantially to volume.

The two most important species in the diet of *H. scapularis*, the amphipod *Probaloides rotunda* and the isopod *Notocellus capensis* were species that occurred very seldom in the food of any of the other fish species examined. No change in diet with increasing size was observed, the same small prey species being equally important in all size classes.

Discussion

Species diversity of the rock-pool fish population in the south western Cape is very high, a Shannon-Weiner diversity index of 2,1 being obtained from a recent survey on the east and west coasts of the Cape Peninsula (Bennett & Griffiths, unpubl.). This value is considerably higher than for fish populations sampled in estuaries (1,1), surf zone (1,4) and offshore demersal (1,6) environments in the same area (Bennett, unpubl.). The high diversity of the rock-pool ichthyofauna is remarkable because of the high biomass (49,60 g m^{-2}) and limited range of feeding types inhabiting the pools, all but one species being small, cryptic carnivores.

The co-habitation of numerous, often closely related, species with similar habitat and dietary requirements gives rise to speculation on the possible competitive interactions occurring between them. This question has received attention from workers studying fish assemblages in other parts of the world. Some consider that Gaussian principles do not apply because food is superabundant (Hartley 1948; Larkin 1956). More recently it has been suggested that interspecific and intraspecific differences in ecology serve to reduce competition for food (Gibson 1972; Keast 1970, 1980).

Superficial examination of Table 2 reveals that amphipods, isopods, and to a lesser extent, polychaetes, were the most important food items consumed by intertidal fishes in the south-western Cape. The first two categories occurred in all species examined and the third in 18 of the 20. Together these three groups comprised more than half the total food consumed by 14 of the species.

Despite the large amount of dietary overlap evident from Table 2, not all the species appear to be in direct competition with each other. Many of the species consume food types that are apparently not important in the diets of the rest of the species. For example, molluscs are consumed in varying amounts by 17 of the species but are of special importance in *Chorisochismus dentex*. Decapods are the single most important category in *Clinus anguillaris* and *C. acuminatus*. Barnacle cirri are found in six species, constituting 43% of the volume consumed by *C. berrisfordi*, but were also important to *C. cottoides* and *C. acuminatus*. Ophiuroids were very seldom found in any of the species, but accounted for 34% of the stomach volume of *C. venustris*; algae were important in the diet of *Caffrogobius caffer* but were considered incidental where they occurred in other species. The intensity of competition between the co-habiting species groups is therefore reduced by virtue of the fact that not all species are relying on the same categories for major parts of their diets.

Competition can be further attenuated if fish species feed on different prey species in a category at different intensities. *Blennioclinus brachycephalus*, for example, eats large amounts of the amphipods *Ampithoe* spp., *Aora typica* and *Caprella scaura*, prey species that only occurred in two other fish species. *Halidesmus scapularis* consumes large amounts of *Probaloides rotunda*, a prey species also consumed by only two other species. *Pavoclinus mus* and possibly *C. brevicristatus* rely to a large extent on *Ischyrocerus anguipes*, a prey species unimportant to any other fish examined.

Thus, although all the co-habiting fish species are reliant on the same food categories, the actual species eaten are subdivided between them. Information collected during this study enabled some explanation of how this subdivision may occur.

Differences in distribution

If the species consistently feed in different areas or habitats, competition between them is likely to be reduced or eliminated.

The distribution and type of habitat in which each species is most commonly found has already been given. From this, it is obvious that not all species are found in any particular area. Species such a *Pavoclinus mus, P. graminis* and *Halidesmus scapularis*, for example, are found only to the east of Cape Point, while others, such as *Clinus capensis* and *Caffrogobius caffer*, are considerably more abundant in this area than they are on the west coast. Other species such as *Clinus agilis, C. heterodon* and *C. venustris* are abundant on the west coast but rare on the east coast. These differences in relative abundance will have a direct bearing on the intensity of competition in a particular area.

Vertical differences in relative abundance are also apparent among species that have overlapping horizontal distributions. Some species, for example *Blennioclinus brachycephalus, P. mus* and *H. scapularis*, are restricted to very low shore areas, while others (e.g. *Caffrogobius caffer* and *Clinus acuminatus*) are characteristically high shore forms. Yet another group which includes *C. superciliosus, C. cottoides* and *C. dorsalis* are found at almost all intertidal levels. Most species are, however, most abundant in the middle and lower regions.

Further separation of the species within a specific area of shore is also possible. In the low shore zone, for example, many species may occur together in a pool but *Pavoclinus* species will be absent unless quantities of algae are present. *Clinus agilis* and *C. brevicristatus* are also invariably absent in pools where there is no weed.

Among the species that do occur within a single pool, body shape may allow further sub-division of the habitat. Elongate species such as *C. anguillaris, C. dorsalis* and *H. scapularis* are able to gain access to considerably smaller holes and crevices than those utilized by all but the very smallest individuals of the more conventionally shaped species, and therefore may exploit different food resources. The differences in relative abundances and apparent habitat preferences outlined in the previous section describe the situation only at low tide, when all sampling was conducted. It is likely that the patterns described will change if the fish feed while submerged by the tide.

Feeding in relation to habitat

Little information on the habitat preferences of prey species is available but it was possible to characterize many of them as weed-dwelling, rock-dwelling or ubiquitous (i.e. likely to be found amongst rock and weed). Differences in the contribution of these three categories to the diet of the different fish species indicate where the majority of feeding takes place.

Clinus acuminatus, C. anguillaris and *Chorisochismus*

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dentex all contained high proportions of prey items classified as rock-dwellers and significant amounts of ubiquitous species, but almost no weed-dwellers. The reverse was found to be true for *P. mus* in which weed-dwelling prey species were overwhelmingly important. Many of the fish species, especially the more abundant ones, contained mixtures of prey from all habitats. In *C. cottoides* and *C. superciliosus* approximately half the stomach contents were rock-dwelling species and one third were weed-dwellers. *Clinus brevicristatus, C. heterodon* and *C. agilis* contained reasonably equal mixtures of rock and weed-dwelling species, but in these species weed-dwellers tended to predominate. The proportions of different food organisms consumed did not always reflect the type of habitat that the fish species were observed to occupy. *Pavoclinus pavo* and *P. graminis*, although apparently occurring exclusively in weedy areas, contained large amounts of prey species that were considered to be characteristically rock-dwelling.

Blennioclinus brachycephalus, which was not considered to be primarily a weed-dweller, appears to obtain most of its food from within algal mats.

Mouth size

The upper size limit of prey that can be taken by a fish is determined by its mouth size (Keast 1970; Yasuda 1960). In this study, mouth sizes of the species examined ranged between 5% (*H. scapularis*) and 16% (*Chorisochismus dentex*) of standard length. The mouth-size distribution showed two modes, one at 8% comprised of two *Pavoclinus* species, *B. brachycephalus* and *Clinus anguillaris* and the other between 11% and 12% with eight *Clinus* species and the two gobies.

All species with mouths smaller than 10% of standard length relied on small food items to a large extent, the amphipod, isopod and polychaete categories providing at least 50% of the total volume consumed. Larger food items such as decapods, most molluscs and echinoderms were usually absent or, if present, found only in the largest individuals. Certain species with larger mouths also relied heavily on small food items such as *C. agilis* and *C. capensis* which continued to consume small items even when they were large enough to prey on the larger species. The high percentage (>65%) of small food items in *C. cottoides* and *C. heterodon* is due to the size distribution of the samples, for in both species juveniles less than 70 mm long predominated.

Since mouth size is related to body length, the size ranges of different species competing for a food particle of particular size will not be the same. For example, the largest particle taken by *H. scapularis* of 100 mm length will be the same as that for *B. brachycephalus* of 63 mm, *C. superciliosus* of 45 mm and *Chorisochismus dentex* of 34 mm. When the size distribution of the population is taken into account, it appears that competition is most intense for small food items and the number of species competing for larger items is considerably smaller.

Changes in diet during growth

The preceding sections have been primarily concerned with interspecific relationships whereas here intraspecific dietary differences are considered. The ability to take larger food items as the fish increase in size is reflected in some species by a change in the species composition of the diet. In this study, it was not possible to assess confidently whether or not changes in diet occurred in all species, because sample sizes or size ranges were in some cases too small.

More than 50 individuals of each of 11 species were examined. Eight (73%) showed changes in diet with increasing size and three continued to eat small species throughout their size range. For an additional four species more than 10 specimens were examined, of which two species showed some indication that larger fish were relying on larger prey species.

Two of the species that did not change diet as they grew (*Clinus capensis* and *C. agilis*) had mouths more than 10% of body length and three, *C. dorsalis, B. brachycephalus* and *H. scapularis* were small-mouthed species that failed to attain a size large enough to enable them to take the larger size-categories of prey.

Conclusions

The results presented in this paper show that although there is considerable dietary overlap among the 20 fish species examined, there is also considerable subdivision of the food resources between them. Much of the observed subdivision is explainable in terms of horizontal and vertical distributional patterns, habitat preferences, mouth size and changes in diet during growth, but the extent to which these factors reduce competition for food is unknown.

It has been pointed out (Hess 1961) that the degree of competition for food between co-habiting species can be ascertained only when population sizes and production rates of both predators and prey species, as well as the rates at which the prey species are consumed, are known. Quantitative data of this nature are at present unavailable for the species under consideration. A rough estimate of annual consumption and food standing stock is, however, possible and allows speculation on factors possibly active in controlling rock-pool fish populations in the south-western Cape.

The mean fish biomass was found to be 49,60 g m^{-2} (wet mass). If daily consumption is considered to be 5% body weight per day (Pandian 1967; Carline & Hall 1973; Bennett 1979) it is evident that approximately 1 000 g m^{-2} $year^{-1}$ is consumed by the fish population. If the prey production : biomass ratio is considered to be 2 : 5 (McLachlan 1977; Koop & Griffiths 1982), then the standing stock must be in the region of 400 g m^{-2}. Although no measurements have been made, this value is considered to greatly exceed the amount of food available. From this, it may be assumed that many of the fish forage outside the pools when they are immersed or that considerable reliance is placed on food that is washed into the pools from the surrounding areas. For this reason, the fish may be considered to be 'concentrated' in the pools at low tide. If this is the case, then the number of pools, their physical complexity or the number of habitat types within pools in a particular shore area, may be factors affecting rocky shore fish communities. Marsh, Crowe & Siegfried (1978) have, in fact, shown significant positive correlations between the amount of cover present and the abundance and diversity of clinids in south-western Cape rock pools. Food, however, probably also plays some role in limiting the fish populations since the degree of dietary overlap relative to the degree of subdivision between the species is appreciable, indicating that some food categories, at least, may be in short supply.

Acknowledgements

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CHAPTER 3.

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A POPULATION ENERGY BUDGET FOR *CLINUS SUPERCILIOSUS* L., WITH AN ASSESSMENT OF THE ROLE OF RESIDENT FISH AS PREDATORS IN THE INTERTIDAL ZONE

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SUMMARY

Clinus superciliosus L. is the most abundant of approximately 20 species of carnivorous fish resident in the rocky intertidal of the southwestern coast of South Africa. By extrapolating the results of laboratory experiments, it is estimated that the naturally occurring *C. superciliosus* population consumes some 110.7 kJ · m^{-2} · yr^{-1} and has a production of 25.6 kJ · m^{-2} · yr^{-1}, giving a gross growth efficiency (K_1) of 0.23. Estimates of respiration, egestion and excretion rates yielded values of 55.1, 22.3, and 7.8 kJ · m^{-2} · yr^{-1} respectively. If it is assumed that the remaining carnivorous fish species have similar energy budgets, total consumption by the intertidal fish community would be about 345 kJ · m^{-2} · yr^{-1}. Since total invertebrate production is estimated to be 14 592 kJ · m^{-2} · yr^{-1}, this would constitute only 2.4% of secondary production. However, only 538 kJ · m^{-2} · yr^{-1} of production is in the form of the small crustacea, molluscs and polychaetes normally taken by the fish, indicating that they exert considerable predation pressure on the available prey.

Key words: energy budget; fish; intertidal.

INTRODUCTION

Attempts have recently been made to derive whole-ecosystem energy flow models from energy budget studies of component species. In South Africa, this approach has been used to provide an understanding of the energy balance in southeastern Cape sandy beach ecosystems and southwestern Cape kelp beds (McLachlan et al., 1981; Newell et al., 1982). An attempt is at present under way to construct a similar model for rocky shores in the southwestern Cape. Estimates of some facets of primary productivity are available (McQuaid, 1980; Cliff, 1982a, b) and the energetics of several primary consumers have received attention (McQuaid, 1980; Branch, 1981; Griffiths, 1981; Koop and Field, 1981). Preliminary studies of predatory invertebrates have also been conducted (Wickens, 1983; Penney and Griffiths, 1984) but of the vertebrate predators, only birds have been studied (Ryan, 1983; Hockey, 1984; Hockey and Underhill, 1984).

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This study is an attempt to assess the role of resident intertidal fish in terms of energy transfer through a rocky shore ecosystem. *Clinus superciliosus* L. was chosen for detailed study since it is the most widely distributed intertidal clinid (Penrith and Penrith, 1983) and over much of its range, the most abundant species (Penrith, 1969, 1970). On the west coast of the Cape Peninsula, it provides approximately half the resident fish biomass (Bennett and Griffiths, 1984). No previous attempts to construct energy budgets for resident intertidal fish species have been made and even estimates of consumption are lacking, thus the quantitative effects of this group of species on rocky shores are virtually unknown (Gibson, 1982).

METHODS

Energy flow through the *C. superciliosus* population was estimated using the standard IBP formulation (Klekowski and Duncan, 1975),

$$C = P + R + F + U$$

which, for the purposes of this study was further subdivided to give

$$C = (P_G + P_R) + (R_S + R_A + R_F) + F + U,$$

where: C = the energy of food consumed, P_G = the energy used in somatic growth, P_R = the energy of reproductive output, R_S = the standard metabolic rate, R_A = the energy expended during activity, R_F = feeding metabolism, and F = energy egested as faeces and U the energy of excreted products.

Consumption, faecal losses and standard metabolic rate were measured directly in the laboratory. Active metabolism and reproductive output were estimated using published data specifically for *C. superciliosus* (Marsh et al., 1978; Veith, 1978), while feeding metabolism and energy lost as dissolved nitrogenous wastes were derived from the literature for other fish species (Brett and Groves, 1979). The energy available for somatic growth was estimated by difference, i.e.

$$P_G = C - (P_R + R_S + R_A + R_F + F + U).$$

All fish used in experimental studies were captured intertidally either by hook and line or hand net. Captive individuals were maintained in the laboratory at 15°C in 180-l glass-fronted fibreglass tanks fitted with gravel filters and through which water was circulated at 2.5 $l \cdot min^{-1}$. Cover in the form of short lengths of P.V.C. piping of different diameters was provided. The fish were fed to satiation twice daily on a selection of invertebrates known to occur in their natural diets (Bennett et al., 1983) and were maintained for a minimum of 25 days before the commencement of experiments.

Feeding experiments

Fifteen fish weighing between 4.37 and 208.40 g (wet mass) were placed separately in 2- to 10-l glass containers. Each container was supplied with bubbling air and water which circulated at a rate equal to the volume of the container every hour. Excess water discharged through a constant level siphon into a 'faeces trap', a smaller container fitted with a 0.25 mm mesh panel which retained the faeces, but allowed the water to drain away.

The mantles of black mussels (*Choromytilus meridionalis*) were the only food used during feeding experiments. They were chosen because they did not disintegrate during handling and were easily distinguished from faeces. Weighed amounts of food were supplied in excess to the fish twice daily, and after one hour unconsumed food was collected and reweighed.

Faeces were collected immediately prior to feeding, by which time most had passed through the constant level siphon and accumulated in the faeces trap. Faeces from the trap or remaining in the main vessel were siphoned out, accumulated on filter paper and dried to constant weight.

In each trial, feeding and faeces collection was carried out for 12 days following an initial 5-day stabilization period.

Standard metabolism

The amount of oxygen consumed by inactive fish after 4 days of starvation was taken as the standard metabolic rate.

Measurements of oxygen consumption were made in 0.5–5.0 l perspex chambers. Each chamber was equipped with inlet and outlet pipes through which water could be circulated. A grid separated the vessel into two compartments, the lower of which contained a magnetic stirring bar. The oxygen content of the water was measured with a YSI model 5739 polarographic oxygen probe connected to a Beckman VLP-12 potentiometric recorder.

Fish were placed individually in the chambers the evening before recordings were made, so that they could acclimate to the new conditions. During this time, a free flow of water was maintained through the chambers. When recording was to commence, the inlet and outlet pipes were sealed and the oxygen concentration of the water monitored for 20 min, or until such time as the oxygen concentration was reduced to 80% of its original value. The chambers were then flushed through until the oxygen concentration stabilized and resealed for a further period of measurement.

Eighteen *Clinus superciliosus* weighing between 0.48 and 210.63 g (wet) were used for the estimation of standard metabolic rate. Experimental temperature was 15°C, the temperature to which this group of fish was acclimated.

RESULTS AND DISCUSSION

Energy budget components

Consumption The amount of food ingested by *C. superciliosus* of different sizes is shown in Fig. 1 and conforms to the equation:

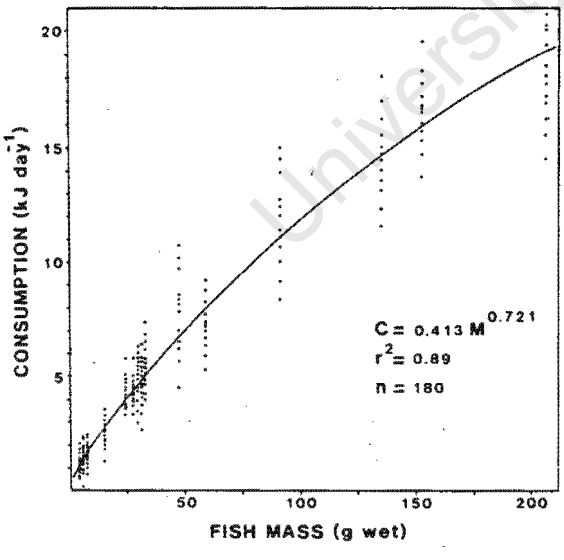
$$^{C}(\text{kJ} \cdot \text{fish}^{-1} \cdot \text{day}^{-1}) = 0.413\ \text{Mass}^{0.721}\ (r^2 = 0.89,\ N = 180).$$

Weight specific rate thus declines with increasing fish size. For example, a 1-g fish ate 9.09% of its body mass per day, a 10-g fish 4.95% and a 100-g fish ate 2.51% (using dry fish mass = 22.5 ± (SD) 1.85% wet mass, $N = 10$; 1 g dry food = 20.20 ± (SD) 0.64 kJ, $N = 6$). These results agree well with published information on the feeding rates of other fish species of equivalent size (tabulated in Conover, 1978; Brett and Groves, 1979).

Faeces The values for energy of solid faecal wastes produced by *C. superciliosus* are shown in Fig. 2. The relationship between rates of faecal production and fish mass is given by the expression:

$$^{F}(\text{kJ} \cdot \text{fish}^{-1} \cdot \text{day}^{-1}) = 0.027\ \text{Mass}^{0.795}\ (r^2 = 0.79,\ N = 180).$$

In fish of all sizes faecal production averaged 9.26% ± 4.88% (SD) of food consumed. This faecal production is similar to reported values for other fish species fed 'soft' food but is probably less than it would have been had a natural diet, consisting



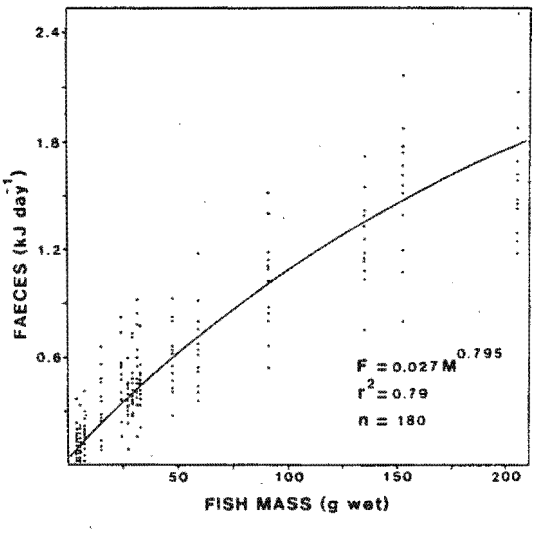


Fig. 1. Daily rates of food consumption (kJ) by *Clinus superciliosus* as a function of fish mass.

Fig. 2. Daily rates of faeces production (kJ) by *Clinus superciliosus* as a function of fish mass.

of food organisms with undigestable exoskeletons, been offered. The reviews of Ivlev (1961) and Brett and Groves (1979) indicate that carnivorous species feeding on mixed invertebrate diets lose approximately 20% of ingested energy as faeces. Thus the relationship between fish size and faeces production by *C. superciliosus* fed on a natural diet may be more closely approximated by assuming an absorption efficiency of 80%, which would give:

$$^{F}(\text{kJ} \cdot \text{fish}^{-1} \cdot \text{day}^{-1}) = 0.083\ \text{Mass}^{0.721}.$$

Urine Early workers assumed that negligible energy was lost via excretion (Winberg, 1956) and for practical reasons, no attempt could be made to estimate this parameter during the present study. Little information on energy loss from nitrogenous excretion by fish is available, but if the mean value of 7% of ingested energy derived by Brett and Groves (1979) is applicable to *C. superciliosus* then dissolved losses would be described by:

$$^{U}(\text{kJ} \cdot \text{fish}^{-1} \cdot \text{day}^{-1}) = 0.029\ \text{Mass}^{0.721}.$$

Standard metabolism The standard oxygen requirements of a size range of *C. superciliosus* are shown in Fig. 3. When converted to energy units (1 mg $O_2 = 0.014$ kJ) the relationship between standard metabolism and fish size becomes

$$^{R}_{S}(\text{kJ} \cdot \text{fish}^{-1} \cdot \text{day}^{-1}) = 0.077\ \text{Mass}^{0.686}\ (r^2 = 0.86,\ N = 108),$$

which gives rates of 1.56 kJ · kg^{-1} · h^{-1} for a 10 g fish and 0.76 kJ · kg^{-1} · h^{-1} for a 100 g fish, values that agree with Brett and Groves' (1979) mean of 1.246 ± 0.476 kJ · kg^{-1} · h^{-1} for several species weighing between 10 and 100 g for which R_S has been 'adequately derived'.

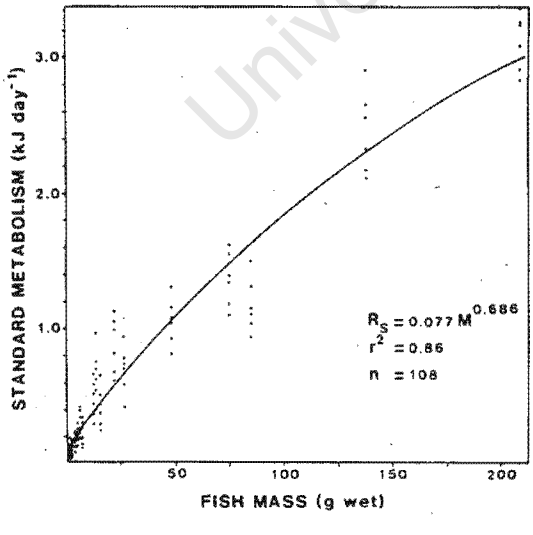


Fig. 3. Standard metabolic rate (kJ · day^{-1}) of *Clinus superciliosus* as a function of fish mass.

Feeding metabolism Energy expenditure during biochemical transformation of ingested food to a metabolizable or excretable form is considered as feeding metabolism (R_F) in this study. Studies on other fish species indicate that approximately 12–15% of ingested energy is used for this purpose (Brett and Groves, 1979). Using the mid-point of this range (14%) one would derive the following:

$$R_F\ (\text{kJ} \cdot \text{fish}^{-1} \cdot \text{day}^{-1}) = 0.058\ \text{Mass}^{0.721}.$$

Activity The use of values derived from other species, together with some knowledge of the biology and behaviour of *C. superciliosus* permits an estimation of the amount of energy expended during routine activity in the natural environment. Active (maximum sustainable) rates of energy utilization by fast swimming, streamlined species are in the region of eight to ten times the standard metabolic rates, but sluggish species would be expected to have a smaller scope for activity (Brett and Groves, 1979). *C. superciliosus* is a cryptic species that spends much of its time inactive, concealed amongst suitable cover. Observation also shows that small individuals are more frequently active than larger ones (Marsh et al., 1978; Bennett and Griffiths, 1984). If we assume the active metabolic rate of this species to be five times its standard rate and that the amount of active time decreases from 6 h a day for small (5 g) individuals to 4 h for large (200 g) individuals, then the relationship between fish size and energy expended during routine activity would be described by

$$R_A\ (\text{kJ} \cdot \text{fish}^{-1} \cdot \text{day}^{-1}) = 0.107\ \text{Mass}^{0.599}.$$

This estimate indicates that daily energy expenditure for activity would approximately equal the standard daily (maintenance) requirement of this species. Other

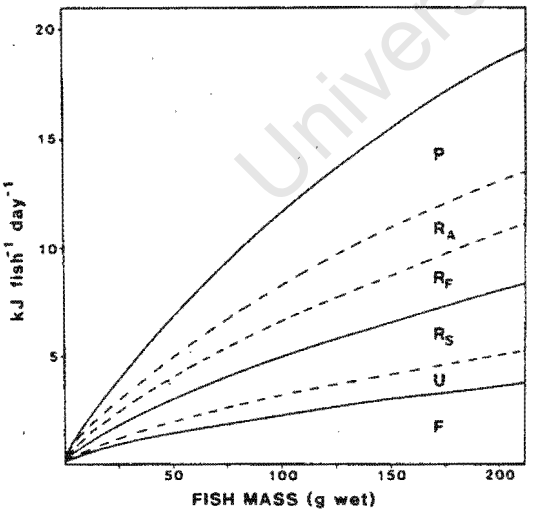


Fig. 4. The relative contribution of each component of the energy budget of *Clinus superciliosus*. The upper curve represents total consumption and the lower curves are plotted cumulatively so that production (P) can be estimated by difference.

authors estimate that energy expended during routine activity is approximately double the standard daily rate (Winberg, 1956; Mann, 1965), but these estimates are for species that are considerably more active than *C. superciliosus*.

Production Estimates of the amount of energy used by *C. superciliosus* in each of the components of its energy budget are plotted cumulatively in Fig. 4. The area remaining between the curve representing total consumption and that representing the sum of the losses gives the amount of energy available for production. Annual size specific production estimated in this way conforms to the equation

$$P(\text{kJ} \cdot \text{g}^{-1} \cdot \text{yr}^{-1}) = 24.87\ \text{Mass}^{-0.164}.$$

This method of estimating production suffers from the drawback that errors in the estimation of other components accumulate in the estimate of production.

Total production may be subdivided into energy used for growth (P_G) and reproduction (P_R). The amount of energy used in reproduction by *C. superciliosus*, an ovoviviparous species, can be estimated from published data on its reproductive biology. Maturation occurs at approximately 18 g wet mass (Jackson, 1950; Penrith, 1965; Veith, 1979) and the number of embryos (NE) in mature females increases linearly with size according to Veith's (1978) equation

$$\text{NE} = 80.80 + 4.287\ \text{Mass}.$$

Broods representing a small proportion of all the embryos in an ovary are born all the year round (Veith, 1979). The gestation period is approximately 2–3 mth (Jackson, 1950; Penrith, 1965; Bennett, 1983) and each prepartum embryo has an energy value of about 0.33 kJ (Veith, 1979). From this information the reproductive output of females of any particular size (Fig. 5) can be calculated. No information on the reproductive output of males is available, but it is likely to be very small relative to that of females. For population budget considerations male reproductive energy output can be ignored since females dominate the larger size classes.

Having obtained values for reproductive output, energy available for growth can

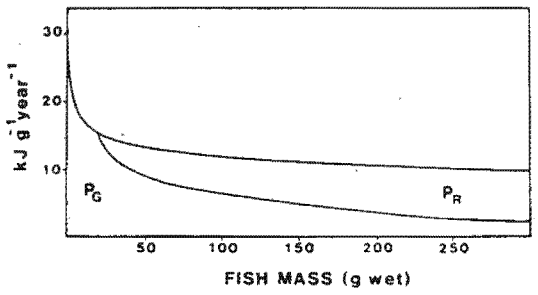


Fig. 5. The subdivision of total production (represented by the upper curve) in *Clinus superciliosus* into energy available for growth (P_G) and reproductive output (P_R) plotted in relation to fish mass.

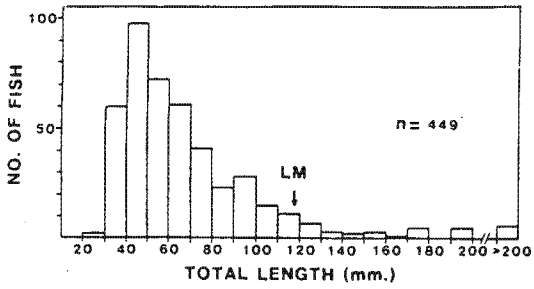


Fig. 6. The length-frequency distribution of *Clinus superciliosus* on the Cape Peninsula. (LM shows the length at which maturity is attained.) Lengths given above may be converted to wet mass (M) using $M = 7.92 \times 10^{-6} L^{3.08}$.

be calculated by difference, since $P_G = P - P_R$ (Fig. 5). This shows that energy available for growth declines to zero as fish size approaches 300 g, which is indeed the maximum size attained by this species (Smith, 1965).

POPULATION ENERGY BUDGET

The abundance and size structure of the *C. superciliosus* population in rock pools around the Cape Peninsula were established by Bennett and Griffiths (1984). Six transects covering 2272 m^2 and incorporating 84 pools with an area of 208 m^2 were sampled. The size distribution of the 449 *C. superciliosus* collected is shown in Fig. 6. Population structure remains unchanged throughout the year (Jackson, 1950; Penrith, 1965, 1970). Juveniles recruit into the intertidal zone when approximately 35 mm in length, mortality and/or emigration is rapid and only a small proportion of the population is mature. Use of the population size structure and the equations relating each energy budget component to mass, enables an energy budget to be calculated for the entire *C. superciliosus* population (Table I). The value of each component is the sum of the values obtained by substituting the mass of each in-

TABLE I

Annual energy budget for the Cape Peninsula *Clinus superciliosus* population. Values are in $kJ \cdot m^{-2} \cdot yr^{-1}$ for the whole intertidal zone and as the percentage of each component of consumption to allow for comparison with the mean energy budget derived by Brett and Groves (1979) which is also shown.

	C =	R_S +	R_A +	R_F +	U +	F +	P
$kJ \cdot m^{-2} \cdot yr^{-1}$	110.67	18.76	20.88	15.49	7.75	22.13	25.57
%	100	17	19	14	7	20	23
			49		27		23
Brett and Groves (1979)	100		44 ± 7		27 ± 3		29 ± 6

Standing stock = 7.17 $g \cdot m^{-2}$.
P/B = 3.6.
K_1 = P/C = 0.23.

dividual fish from the field sample into the equations relating the energy budget components to mass.

The agreement of estimates for components of the energy equation made in this study with published results has already been pointed out. Brett and Groves (1979) calculated a 'mean energy budget' for carnivorous fish based on a review of laboratory studies of fish which were fed at above maintenance levels at normal temperatures. The relative contributions of each of the energy budget components estimated for *C. superciliosus* all fall within the 95% confidence limits of the mean budget derived by Brett and Groves (Table I). Thus, despite the problem of having to estimate some elements of the energy budget of *C. superciliosus* from figures in the literature, confidence can be placed in the results although, of course, there is considerable doubt as to the validity of applying such laboratory estimates to natural populations (Warren and Davis, 1967; Healey, 1972; Conover, 1978).

IMPORTANCE OF *CLINUS SUPERCILIOSUS* AS AN INTERTIDAL PREDATOR

Annual consumption of the Cape Peninsula *C. superciliosus* population is estimated to be 110.7 $kJ \cdot m^{-2}$ of intertidal zone. Available information on secondary production in the same area enables an assessment of the importance of *C. superciliosus* as a predator on rocky shores.

McQuaid (1980) estimated the mean dry biomass of rocky shore invertebrates on the Cape Peninsula as 352 $g \cdot m^{-2}$, from which Field (1983) estimated total annual production to be 746 $g \cdot m^{-2}$ or 14 592 $kJ \cdot m^{-2}$. *C. superciliosus* would thus consume about 0.76% of invertebrate production. This might suggest that *C. superciliosus* plays a minor role as a consumer. However, only a small proportion of total invertebrate biomass is available to *C. superciliosus*. Analysis of stomach contents shows that this species eats primarily small crustaceans, polychaetes and molluscs (Bennett et al., 1983). Closer examination of McQuaid's (1980) figures reveals that the majority (96.8%) of invertebrate biomass comprises organisms such as limpets, barnacles and bivalves which, by virtue of their large size, firm attachment to the substratum and/or protective coverings, are seldom consumed by *C. superciliosus*. Thus almost the entire predation pressure by this species is borne by small mobile crustacea, polychaetes and molluscs, which together comprise only 3.2% of total dry biomass, or 11 $g \cdot m^{-2}$. If this 'available' group is assumed to have a P/B ratio of 2.5 (McLachlan, 1977; Koop and Griffiths, 1982) and a mean energy content of 19.56 $kJ \cdot g^{-1}$ (Field, 1983), then available production is in the region of 535 $kJ \cdot m^{-2} \cdot yr^{-1}$. Since *C. superciliosus* consumes 110.7 $kJ \cdot m^{-2} \cdot yr^{-1}$, this in fact constitutes some 21% of available prey, making the species an important predator of small crustacea, polychaetes and molluscs.

At least 20 other fish species reside in rock pools on the Cape Peninsula. All are small, cryptic and, with the exception of *Caffrogobius caffer* and *Chorisochismus dentex*, consume the same type of prey as *Clinus superciliosus* (Bennett et al., 1983).

Since the abundance and size structure of these species are known (Bennett and Griffiths, 1984; Bennett, unpublished data), an assessment of their role as consumers can also be made, if it is assumed that, weight for weight, their consumption and production is similar to that of *C. superciliosus*. On this basis, the entire resident intertidal fish community (including *C. superciliosus*) would consume about 2.4% of total invertebrate production. Further, if the spectrum of prey available to all the fish species were the same as that utilized by *C. superciliosus*, approximately 64% of the production of small crustaceans, polychaetes and molluscs would be consumed by resident fish.

We have no data on the effects of this intense predation pressure on prey species, although intertidal fish elsewhere are known to profoundly influence the population structure of their prey. *Oligocottus maculosus,* for example, is capable of eliminating the copepod *Tigriopus californicus* from tide pools (Dethier, 1980) and *Blennius pholis* may be responsible for maintaining colour polymorphism in *Littorina mariae* (Reimchen, 1979).

The large proportion of prey production taken by intertidal fish also implies that the fish compete intensely for available resources and that population size may be food limited. Analysis of stomach contents (Bennett et al., 1983) and distribution patterns (Bennett and Griffiths, 1984) support this contention in that they demonstrate that the various species tend to avoid competition by specializing both their feeding habits and habitat preferences. The number of fish that can be supported is, however, also strongly dependent upon the distribution and degree of shelter available in the rock pools present (Bennett and Griffiths, 1984) and this constraint may limit the fish populations at levels below that at which food becomes limiting.

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CHAPTER 4.

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The rock-pool fish community of Koppie Alleen and an assessment of the importance of Cape rock-pools as nurseries for juvenile fish

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Fishes inhabiting rock-pools at Koppie Alleen on the southern Cape coast were collected quarterly over two years. Clinids (10 species) were numerically dominant with *Clinus cottoides* (63,4%) and *C. dorsalis* (8,5%) being the most abundant species. Five other species, namely *C. superciliosus, Chorisochismus dentex, Kuhlia mugil, Liza richardsoni* and *Diplodus sargus* each constituted more than 2% of the sample. Species richness varied seasonally, being greater during the summer months owing to an influx of transient species. Comparisons with the eastern and western Cape fish faunas reveal an eastward increase in the total number of species, in the number of subtropical species and in the contribution of transient species, and substantiates previous observations on trends in the composition of the resident component. The importance of the Cape rock-pool habitat as a nursery area is assessed by comparing the abundance of the fish in rock-pools with available information on other inshore habitats. No species were found to be entirely dependent on rock-pools as a juvenile nursery area although *Acanthistius sebastoides, Epinephelus guaza, Sparodon durbanensis, Diplodus cervinus, Cheilodactylus fasciatus* and *Chirodactylus brachydactylus* appear to make some use of this habitat.

Visse wat in rotspoele te Koppie Alleen aan die Suid-Kaapse kus voorkom, is driemaandeliks vir 2 jaar gekollekteer. Kliniede (10 spesies) was die numeries oorheersende groep, waarvan *Clinus cottoides* (63,4%) en *C. dorsalis* (8,5%) die volopste was. Vyf ander spesies, naamlik *C. superciliosus, Chorisochismus dentex, Dules taenarius, Liza richardsoni* en *Diplodus sargus* het elk tot meer as 2% van die getalle bygedra. Spesiesrykheid het seisoenaal gewissel en was hoër gedurende die somermaande as gevolg van die instroming van tydelike spesies. Vergelykings met Oos- en Wes-Kaapse visfaunas dui 'n ooswaartse toename van die totale aantal spesies, van die aantal subtropiese spesies en die bydrae van die tydelike spesies aan, en bevestig vorige waarnemings oor neigings in die samestelling van die permanente komponent. Die belangrikheid van die Kaapse rotspoelhabitat as 'n kweekgebied word beraam deur die getalrykheid van vis in die rotspoele te vergelyk met gepubliseerde gegewens oor ander aanlandige habitatte. Geen spesie is gevind wat ten volle afhanklik van die rotspoelhabitat as 'n kweekgebied is nie, alhoewel dit blyk dat *Acanthistius sebastoides, Epinephelus guaza, Sparodon durbanensis, Diplodus cervinus, Cheilodactylus fasciatus* en *Cheirodactylus brachydactylus* hierdie habitatte op groot skaal gebruik.

The occurrence of juvenile marine fishes in habitats not frequented by their adult populations has recently been examined by a number of workers around South Africa. Estuaries have become well known as important nursery areas (e.g. Wallace & van der Elst 1975; Day, Blaber & Wallace 1981; Wallace, Kok, Beckley, Bennett, Blaber & Whitfield 1984), with an estimated 41 species being largely or wholly dependent on this habitat (Wallace *et al.* 1984). The surf zone of sandy beaches (Lasiak 1981, 1983), surf zone reefs (Berry, van der Elst, Hanekom, Joubert & Smale 1982) and shallow areas with soft substrata (Smale 1984; Buxton, Smale, Wallace & Cockcroft 1984) have all been shown to act as nursery areas for a wide variety of species. Most recently Beckley (1985a, b, c) has presented evidence to suggest that in the eastern Cape rock-pools are an important nursery for at least four species, two of which are significant in the recreational linefishery.

Research on the fish inhabiting rock-pools was initially directed at their taxonomy and distribution (Smith 1945, 1947, 1960, 1965; Penrith 1965, 1969, 1970, 1976; Penrith & Penrith 1972, 1983; Winterbottom 1976). More recently the biology of selected species (Christenson 1978a, b; Veith 1979; Stobbs 1980; Butler 1982; Bennett, Griffiths & Penrith 1983; Bennett 1985) and the structure of their communities (Jackson 1950; Marsh, Crowe & Siegfried 1978; Christensen & Winterbottom 1981; Beckley 1985a, 1985b; Bennett & Griffiths 1984; Bennett 1985), have been examined.

Quantified information on the species composition and abundance of the fishes inhabiting rock-pools is available for four localities around South Africa, two in the western Cape described by Bennett & Griffiths (1984) and two in the eastern Cape described by Christensen & Winterbottom (1981) and Beckley (1985a). This paper describes the fish community at Koppie Alleen in the southern Cape, compares it with those in the eastern and western Cape and with available information on the fish communities in adjacent shallow marine habitats. Its aims are to analyse the changes in the species composition and abundance that take place around the Cape coast and to review the importance of this habitat as a nursery for juvenile marine fishes.

Study site

Koppie Alleen is situated approximately 50 km east of Cape Agulhas on the coast of the De Hoop nature reserve (Figure 1). The coastline lies WSW to ENE and consequently is exposed to the prevailing oceanic swells from the south-west. Semi-diurnal tides with a mean range of approximately 0,55 m at neaps and 1,60 m at springs are experienced. Sea temperatures have an approximate range of 14–24°C.

The intertidal zone at Koppie Alleen is a horizontal wave-cut aeolianite platform up to 50 m wide. It is backed by broken cliffs up to 10 m in height and, at its seaward edge, it drops away almost vertically to a sandy sea bed 3–4 m below. The platform is penetrated by numerous gullys, many of which reach almost to the cliff base. The average height of the platform is slightly above the MHWN level but the most conspicuous invertebrates are *Perna perna, Chthalamus dentata, Tetraclita serrata, Pomatoleios kraussi* and *Patella granularis*, species more characteristic of mid-shore levels.

Numerous rock-pools of varying sizes are scoured into the platform. Typically these have almost vertical sides with few holes and crevices, the bottoms are usually flat and often covered by sand, occasionally with small quantities of pebbles

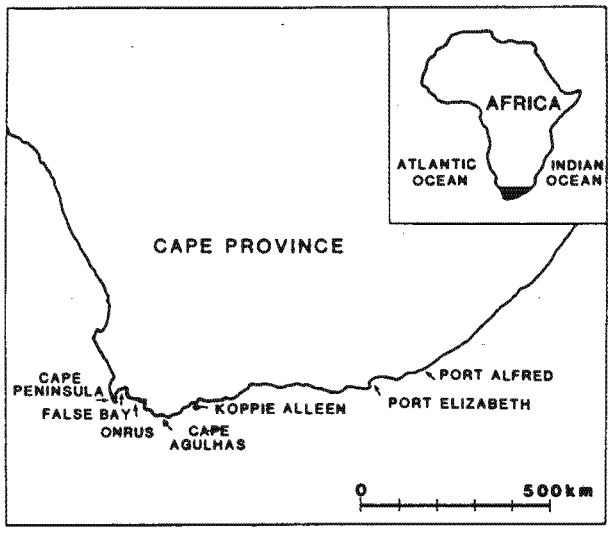

Figure 1 Map showing the location of the sampling site and other places mentioned in the text.

and shells present. None of the pools warranted a rock cover index of more than two on the scale described in Bennett & Griffiths (1984). The rims of most pools, or the entire pools, if they were shallow and on the seaward edge of the platform, were covered by *P. perna*. Below the *P. perna* rim the sides were covered by a variety of algae. A number of coralline species were abundant and usually covered a large proportion of the pools' sides. Other common and conspicuous algae were *Sargasum heterophyllum, Ecklonia radiata, Cytophora fibrosa* and *Bifucariopsis capensis*.

Methods

Collection of fish from the rock-pools on the intertidal platform at Koppie Alleen were made every three months between May 1984 and February 1986. On each occasion between 7 and 10 pools were selected so that they were representative of the whole platform in terms of size, distance from the seaward edge and the amount of rock and algal cover present. Care was taken to ensure that at least 12 months had elapsed before any pool was re-sampled. The ichthyocide rotenone (dissolved in acetone) was added to each pool and the fish then collected with hand nets. Fish from each pool were preserved separately in 10% formalin. Each fish was subsequently identified and measured to the closest mm (total length) and each species from each pool was batch weighed (wet) with an accuracy of 0,01 g.

Results

A total of 2595 fish of 21 species representing nine families was collected from 61 rock-pools which had a total surface area of 483,85 m^2 (Table 1). The average density in the pools was 5,36 fish or 20,75 g m^{-2}.

Clinids (10 species) were numerically dominant comprising 78,4% of the sample with *Clinus cottoides* (63,4%) and *C. dorsalis* (8,5%) being the most abundant species. Five other species namely *C. superciliosus, Chorisochismus dentex* (Gobiesocidae), *Kuhlia mugil* (Kuhlidae), *Liza richardsoni* (Mugilidae) and *Diplodus sargus* (Sparidae) each accounted for more than 2% of the sample. The community is therefore composed mainly of cryptic species (clinids and *C. dentex*) which spend most of their time concealed amongst rock and weed cover but shoaling species such as *K. mugil, L. richardsoni* and *D. sargus* were also of some importance.

From the size frequency distributions shown in Figure 2 and the data in Table 1 it is evident that all fish inhabiting the rock-pools were small, over 90% being under 100 mm long. The sample covers the full size range of a number of small species as well as the juveniles (defined here as immature or individuals of < 100 mm) of larger species. Thirteen of the species occurred as adults, all, with the exception of *Atherina breviceps*, being the small cryptic species typical of the resident rock-pool fauna. The remaining eight species occurred only as juveniles and of these *Cheilodactylus fasciatus, Chirodactylus brachydactylus, K. mugil, L. richardsoni, D. sargus* and *Sarpa salpa* have their adult populations in other marine habitats.

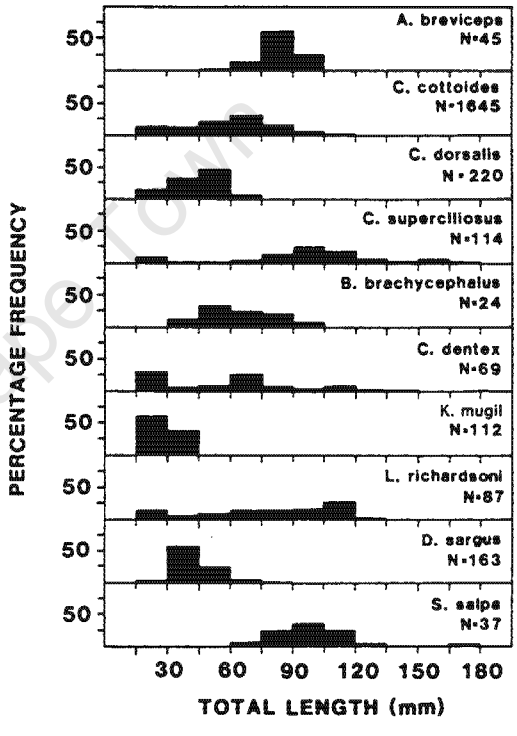

Figure 2 Size frequency distributions of the ten most abundant fish species sampled from rock-pools at Koppie Alleen.

Seasonal changes in the rock-pool community were evident (Figure 3). The number of species varied through the year being highest during the late summer and lowest in the winter and spring. The number of species present as both adults and juveniles varied only slightly (between six and eight) and showed no seasonal trend whereas the species present only as juveniles numbered between one and five and were most abundant in February and May (Figure 3).

Almost all the species collected from the rock-pools at Koppie Alleen are endemic to southern Africa, the only exceptions being *Diplodus sargus* and *Sarpa salpa*, which have circum-African distributions, and *Kuhlia mugil* which is an Indo-Pacific species. Four of the species recorded were beyond their previously known distributional ranges — *Clinus acuminatus* and *C. berrisfordi* have not been recorded east of Cape Agulhas and Onrus respectively (Penrith 1970) whereas *Blennioclinus stella* has not been recorded west of Port Elizabeth (Penrith 1970; Beckley 1985a) and *K. mugil* west of Mossel Bay (van der Elst 1981). These new distribution records

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Table 1 Species of fish collected in intertidal pools at Koppie Alleen over a two-year period with details of their numerical abundance, seasonality, size and whether they were present as adults (A) and/or juveniles (J)

Family	Species	Number	% *N*	Length range (mm)	Mean length (mm)	*S.D.*	Adult/ juvenile	Summer winter
Atherinidae	*Atherina breviceps*	45	1,73	45 – 100	86,7	16,3	A,J	S
Blenniidae	*Parablennius cornutus*	17	0,66	55 – 91	71,8	9,9	A,J	S,W
Cheilodactylidae	*Cheilodactylus fasciatus*	9	0,35	66 – 172	126,0	29,3	J	S,W
	Chirodactylus brachydactylus	19	0,73	44 – 131	90,4	21,4	J	S,W
Clinidae	*Blennioclinus brachycephalus*	24	0,92	38 – 94	66,1	20,0	A,J	S,W
	B. stella	10	0,39	19 – 44	35,5	9,1	A,J	S,W
	Clinus acuminatus	1	0,04	66				
	C. berrisfordi	4	0,15	75 – 83	78,8	3,5	A,J	S,W
	C. capensis	1	0,04	76				
	C. cottoides	1645	63,39	20 – 105	58,3	20,2	A,J	S,W
	C. dorsalis	220	8,48	25 – 67	43,5	14,2	A,J	S,W
	C. superciliosus	114	4,39	20 – 185	93,6	27,0	A,J	S,W
	Pavoclinus graminis	8	0,31	69 – 132	104,1	28,9	A,J	S,W
	P. pavo	8	0,31	22 – 78	47,1	20,1	A,J	S,W
Gobiesocidae	*Chorisochismus dentex*	69	2,66	16 – 145	60,7	25,2	A,J	S,W
Gobiidae	*Caffrogobius saldanha*	1	0,04	21				
	Psammogobius knysnaensis	1	0,04	28				
Kuhlidae	*Kuhlia mugil*	112	4,32	21 – 40	25,9	6,1	J	S
Mugilidae	*Liza richardsoni*	87	3,35	24 – 134	81,4	27,2	J	S
Sparidae	*Diplodus sargus*	163	6,28	21 – 102	46,0	11,9	J	S,W
	Sarpa salpa	37	1,43	77 – 171	98,3	26,2	J	S

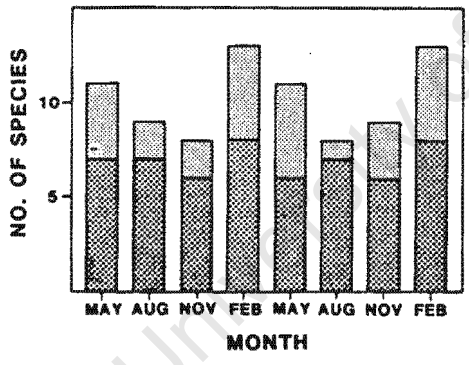

Figure 3 Seasonal variation in the number of transient (light shading) and resident (dark shading) species of fish sampled at Koppie Alleen. Vagrant species that were present in only one sample are omitted.

illustrate the paucity of previous sampling in rock-pools in the southern Cape.

Discussion

Information on rock-pool fishes similar to that given for Koppie Alleen in this paper is available for four other localities on the South African coast. Two of these localities (described by Bennett & Griffiths 1984) are in the western Cape, on the coasts of False Bay and the western Cape Peninsula, and two are in the eastern Cape, one near Port Elizabeth (Beckley 1985b) and the other north of Port Alfred (Christensen & Winterbottom 1981). Koppie Alleen's position in the southern Cape fills a gap in our knowledge of the geographical distribution of intertidal fish communities and allows comparisons to be made around the Cape coast.

A list of the 65 species collected, together with their relative abundance in each of the five localities, is given in Table 2. Included in this table is a classification of the fish into transient and resident species. This subdivision, based on a variety of criteria, has been used by numerous authors worldwide (see Gibson 1969, 1982 for reviews). For the purposes of this study species are classified as residents if they breed in rock-pools and are found there as both adults and juveniles. Transient species may occur in rock-pools seasonally or year-round but typically only as juveniles — they breed and have their adult populations elsewhere. Species that were collected in only one of the five localities and contributed less than 2% to the sample in that locality are not classified.

Twenty (95%) of the 21 common resident species are endemic to southern Africa. Three of them range from the cool waters of the west coast to the warm east coast but most have fairly restricted distributions, nine are found only on the west and south coasts, six on the south and east coasts and three are confined to the southern Cape. The transient species have considerably wider distributions. Eight of them (53%) are endemic to southern Africa but, of the remaining seven species, four have circum-African or Atlantic distributions and three are Indo-Pacific species. The average distribution range of the endemic resident species is approximately 1500 km and that of the endemic transients is more than 2400 km. This difference between residents and transients (it would be considerably greater if non-endemic species were considered) suggests that the resident species, all of which have some reproductive specialization to limit dispersal (e.g. viviparity, benthic eggs and reduced larval phases) are specifically adapted to the rock-pool environment in a particular area whereas most transients are tolerant of a wider range of environmental conditions.

Some of the rarer species i.e. those which were not classified in Table 2, may be genuinely rare intertidal residents (e.g. *Clinus brevicristatus*) whereas others such as *C. venustris, C. taurus* and *Eckloniaichthyes scylliorhiniceps* may breed intertidally but their major populations are subtidal. Most, however, would be accurately described as transient vagrants from

Table 2 The occurrence and relative abundance of the fish species sampled from five localities around the Cape coast and their classification into residents (R) or transients (T) (*, ** and *** indicate whether they comprised <2%, 2–6% or >6% of the sample; species which occurred at only one locality and provided <2% of the sample are not classified)

Species	Family	Peninsula West coast	False Bay	Koppie Alleen	Port Elizabeth	Port Alfred	Resident/transient
Clinus agilis	Clinidae	***					R
C. heterodon	Clinidae	***					R
C. venustris	Clinidae	*					
Eckloniachthys schliorhiniceps	Gobiesocidae	*					
Clinus brevicristatus	Clinidae	*					
C. anguillaris	Clinidae	*	*				R
C. acuminatus	Clinidae	***	*	*			R
C. dorsalis	Clinidae	***	**	***			R
Chorisochismus dentex	Gobiesocidae	***	***	**	*		R
Blennioclinus brachycephalus	Clinidae	*	*	*	*	*	R
Caffrogobius caffer	Gobiidae	**	***		***	**	R
Clinus cottoides	Clinidae	***	***	***	***	**	R
C. superciliosus	Clinidae	***	***	**	***	***	R
C. taurus	Clinidae		*				
Pavoclinus pavo	Clinidae		*	*			R
Clinus berrisfordi	Clinidae		*	*			R
Cheilodactylus fasciatus	Cheilodactylidae		*	*	*		T
Clinus capensis	Clinidae		**	*	*		R
Pavoclinus mus	Clinidae		*		*		R
Halidesmus scapularis	Congrogadidae		**		**		R
Galeichthys feliceps	Ariidae		*		*	**	T
Psammogobius knysnaensis	Gobiidae			*			
Blennioclinus stella	Clinidae			*	*		R
Pavoclinus graminis	Clinidae			*	**		R
Atherina breviceps	Atherinidae			*	***		T
Caffrogobius saldanha	Gobiidae			*	***	*	R
Chirodactylus brachydactylus	Cheilodactylidae			*	***	*	T
Liza richardsoni	Mugilidae			**	**	?	T
Diplodus sargus	Sparidae			***	***	***	T
Parablennius cornutus	Blenniidae			*	*	***	R
Kuhlia mugil	Kuhlidae			**		*	T
Sarpa salpa	Sparidae			*		*	T
Chaetodon marleyi	Chaetodontidae				*		
Monishia william	Gobiidae				*		
Omobranchus woodi	Blenniidae				*		
Pavoclinus laurentii	Clinidae				*		
Coccotropis gymnoderma	Scorpaenidae				*		
Arothron inconditus	Tetradontidae				*		
Sparodon durbanensis	Sparidae				**		T
Liza dumerili	Mugilidae				*	?	
Liza tricuspidens	Mugilidae				*	?	
Acanthistius sebastoides	Serranidae				*	*	T
Diplodus cervinus	Sparidae				*	*	T
Conger wilsoni	Congridae				*	*	T
Amblyrhyncotes honckenii	Tetradontidae				*	*	T
Parablennius pilicornis	Blenniidae				*	*	R
Rhabdosargus holubi	Sparidae				**	*	T
Epinephelus guaza	Serranidae				*	**	T
Scartella emarginata	Blenniidae				*	**	R
Gymnothorax undulatus	Muraenidae					*	
Nannocampus elegans	Syngnathidae					*	
Epinephelus flavocaeruleus	Serranidae					*	
E. spiniger	Serranidae					*	
Pomadasys olivaceum	Pomadasyidae					*	
Lithognathus lithognathus	Sparidae					*	
Pseudupeneus rubescens	Mulidae					*	
Abudefduf saxitalis	Pomacentridae					*	

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Table 2 continued

Species	Family	Peninsula West coast	False Bay	Koppie Alleen	Port Elizabeth	Port Alfred	Resident/transient
Stethojulis interrupta	Labridae					*	
S. trilineata	Labridae					*	
Istiblennius edentulus	Blenniidae					*	
Omobranchus banditus	Blenniidae					*	
Charibarbitus celetus	Callionymidae					*	
Quisquilius cinctus	Gobiidae					*	
Heteromycteris capensis	Soleidae					*	
Synaptura marginata	Soleidae					*	
Number of fish sampled		1028	513	2595	3073	1014	

other faunal provinces or adjacent marine habitats. Individually these species do not contribute significantly to the rock-pool fish fauna but, as a group, they may be important.

From Table 2 and Figure 4A it is apparent that there is an eastward increase in the number of species sampled and that the species composition changes markedly. Before considering these trends the influence of the physical characteristics of the rock-pools that were sampled in each area and the time of year that sampling was conducted should be mentioned since the five samples shown in Table 2 are not identical in these respects. The pools on the western and False Bay coasts of the Cape Peninsula were selected to include the full size range of pools available, all shore heights and a wide range of rock and algal cover. In comparison those at Koppie Alleen, although representative of all available pools, were fairly uniform in size, had low values for cover and were all from mid-shore. The eastern Cape pools were all large and low on the shore but with unspecified amounts of cover. It has been shown that the diversity and abundance of fish is greatest in low-shore pools, in larger pools or in those containing more cover and that different species occur at different shore levels and amongst specific types of cover (Bennett *et al.* 1983; Bennett & Griffiths 1984). This lack of consistency between samples from the different localities may lead to under- or over-representation of certain species according to whether or not their specific requirements are met in that locality. The timing of sampling is also likely to be important especially in relation to the degree to which the transient species are represented since their reproductive cycles and the prevailing water temperatures and ocean currents will affect their recruitment into rock-pools. Thus, in comparison with the Port Elizabeth and Koppie Alleen samples which were taken throughout the year, transients will be over-represented in the Port Alfred sample, which was taken during the summer months, and under-represented in the Cape Peninsula samples which were collected during the winter months only. Despite these inconsistencies in sampling it is considered that the samples are a reasonably accurate reflection of the fish

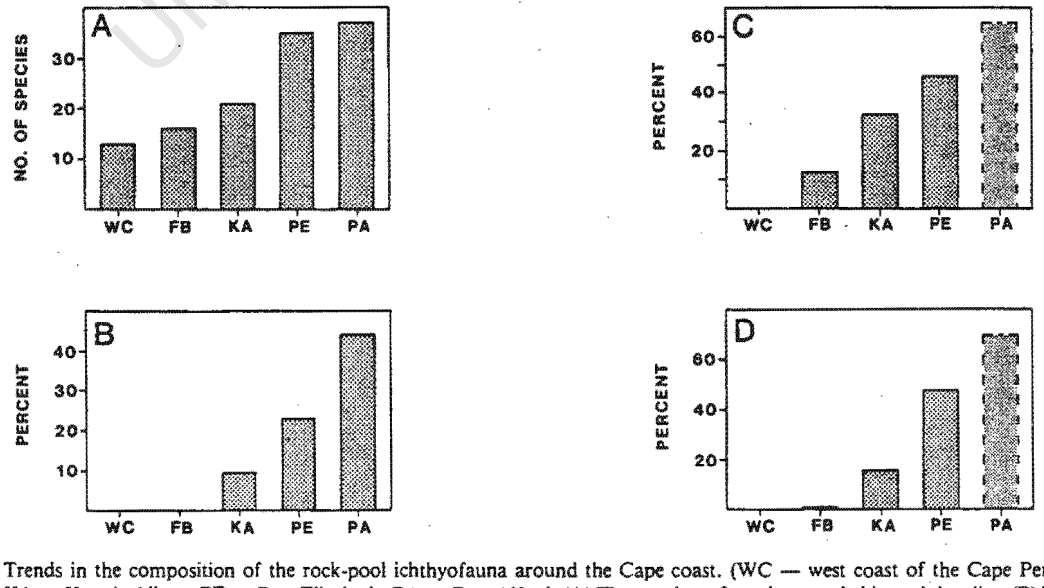

Figure 4 Trends in the composition of the rock-pool ichthyofauna around the Cape coast. (WC — west coast of the Cape Peninsula, FB — False Bay, KA — Koppie Alleen, PE — Port Elizabeth, PA — Port Alfred. (A) The number of species sampled in each locality. (B) The percentage of subtropical species in each sample. (C) The percentage of species which were represented only by juvenile individuals (transient species). (D) The percentage of the number of fish sampled in each locality that were species present only as juveniles in that locality. The percentages given for Port Alfred in (C) and (D) are estimates.

communities inhabiting each of the five localities around the coast and that comparisons between them are valid.

Penrith (1970) has examined the distribution of resident species, particularly the clinids, around southern Africa giving estimates of their relative abundance in different regions. Her observation that clinids, particularly *Clinus superciliosus* and *Clinus cottoides* together with *Chorisochismus dentex* and *Caffrogobius caffer*, dominate the resident rock-pool fish fauna on the western and southern Cape coasts with blennies and gobies increasing in prominence from the south-eastern Cape northwards are substantiated here. The distribution and abundance of transient species around the southern African coast has received very little attention and, from Table 2, it would appear that this is the group which is primarily responsible for the eastward increase in species richness. The number of species that were represented only by juvenile individuals increased from zero on the west coast, through two in False Bay, seven at Koppie Alleen and sixteen at Port Elizabeth to twenty-four near Port Alfred (Figure 4C, D). This is an increase of from 0 – 65% in the number of species and from 0 – 70% in the total number of individuals sampled in each locality. This trend is consistent with that well established in the biogeographical literature i.e. species richness decreases polewards, correlated with decreasing temperatures (Eckman 1954; Briggs 1974). A major feature of this trend in species richness is the marked eastward increase in the numbers of subtropical species present in Cape rock-pools (Figure 4B). This is probably primarily due to the increasing influence of the Agulhas current which flows from the warm waters of the species-rich tropical Indian Ocean thereby facilitating the southward transport of the early life stages of these species. No species from subtropical West African waters occurred on the west coast probably because of the northward flow of the Benguela current and the intervening cold waters and long stretches of sandy beach.

Thirty-two of the species recorded from Cape rock-pools were found in only one locality and constituted less than 2% of the sample. In view of their scarcity it is not possible to assess their degree of dependence on rock-pools but it is unlikely that this habitat performs an important nursery function for them. Many of the primarily subtropical species such as blennies, labrids, serranids, pomacentrids and the more abundant *Kuhlia mugil* approach their southern distribution limits in the south-eastern Cape. At the centre of their distributions these species may be abundant in rock-pools and inshore waters but at their southward extension they may be entirely dependent on rock-pools. This phenomenon has been observed for corals and other subtropical marine animals and attributed to solar warming of the pools (Day 1969). Thus the species near their southern distribution limits may depend on rock-pools for their presence in the Cape but the fact that their populations are centred elsewhere suggests that Cape rock-pools are unlikely to be significant to these species.

The species most likely to be dependent on rock-pools as juveniles are the 15 listed as transients in Table 2. The biology and distribution patterns of seven of them, *Amblyrhynchotes honckenii, Galeichthys feliceps, Atherina breviceps, Diplodus sargus, Liza richardsoni, Rhabdosargus holubi* and *Sarpa salpa* are reasonably well known. Important nursery areas for these species appear to be estuaries for *A. breviceps* and *R. holubi*, the surf zone of sandy beaches for *L. richardsoni*, shallow inshore waters with soft substrata for *G. feliceps* and the surf zone for *A. honckenii* and *D. sargus* (Lasiak 1981; Buxton *et al.* 1984; Wallace *et al.* 1984; Beckley 1985c; Bennett in prep.). Rock-pools are not important nurseries for any of them.

Acanthistius sebastoides, Conger wilsoni and *Epinephelus guaza* are more difficult to assess because they are cryptic, sedentary reef species which are difficult to count. The apparent scarcity or absence of these species subtidally (Christensen 1976; Zoutendyk 1982; Buxton & Smale 1984; Beckley 1985c; Bennett in prep.) may therefore be an artefact of the visual census methods used. It is possible, however, that these species are dependent on rock-pools as nurseries and follow the pattern observed by Berry *et al.* (1982) for *E. andersoni* which moves from the shallows onto deeper reefs when sub-adult. This pattern has also previously been suggested by Beckley (1985b) for *E. guaza* and may hold for other species.

The remaining four transient species, *Sparodon durbanensis, Diplodus cervinus, Cheilodactylus fasciatus* and *Chirodactylus brachydactylus* are all considered by Beckley (1985b) to 'rely extensively and possibly exclusively, on tidal pools as nursery areas'. Her conclusion conflicts with much of the available information concerning these species and necessitates a detailed re-assessment of their dependence on the rock-pool nursery.

Sparodon durbanensis is endemic to the Cape although adults do occur on the Natal coast during the winter. It is an inshore species which is usually encountered over rocky substrata at less than 20 m where the adults are much sought after by anglers and spearfishermen. Although considered to be common by van der Elst (1981) and Smith & Smith (1966) this is contrary to the observations of Day, Field & Penrith (1970), Beckley (1985c), Christensen (1976) and Bennett (in prep.) who all list this species as only rare or present. *Sparodon durbanensis* spawns during the winter and early spring (van der Elst 1981) and juveniles are evident in rock-pools (Christensen 1976; Beckley 1985; Day *et al.* 1970) and in shallow subtidal areas (Buxton & Smale 1984; Beckley 1985c; Christensen 1976; Bennett in prep.). No juveniles occurred in the rock-pools sampled in the south-western Cape by Bennett & Griffiths (1984) or Jackson (1950), or at Koppie Alleen although their presence in very low numbers is recorded by Day *et al.* (1970). Diving observations, on the other hand, show them to be abundant in the southern Cape (Buxton & Smale 1984) and present in the south-western Cape (Bennett in prep.). From this is would appear that in the southern and south-western Cape, rock-pools have no importance as nurseries for this species, the few individuals that are occasionally encountered being merely visitors from shallow subtidal reefs. Information from the eastern Cape shows no clear picture. Beckley (1985b) found small juveniles of this species to be common intertidally at her study site near Port Elizabeth whereas further north they were found to be rare (Christensen 1976) or absent (Christensen & Winterbottom 1981). The importance of eastern Cape rock-pools as nurseries for *S. durbanensis* cannot therefore be clearly assessed but it is considered that Beckley (1985a) overstressed the importance of this habitat since juveniles were common in only one of the three localities sampled in the area.

Diplodus cervinus, also a linefish species, is common on inshore reefs. They breed during the spring and juveniles are present both inter- and sub-tidally (van der Elst 1981). Like *S. durbanensis*, this species is also considered by Beckley (1985a) to be dependent on rock-pool nurseries but, again, juveniles were absent from the southern and south-western Cape rock-pool samples although their presence was recorded by Day *et al.* (1970) and Jackson (1950). In the eastern Cape

they are rare in the samples of Beckley (1985a) and Christensen & Winterbottom (1981) but considered common by Christensen (1976). Subtidally juveniles are listed as common by Christensen (1976), Beckley (1985c) and Bennett (in prep.) and abundant by Buxton & Smale (1984). On the basis of this information it seems that *D. cervinus* is not dependent on rock-pool nurseries to any great extent although it does make extensive use of them, especially in the eastern Cape.

The same information as that used to establish the relative importance of rock-pools and shallow reef areas for *S. durbanensis* and *D. cervinus* is available for *C. fasciatus* and *C. brachydactylus*. Juveniles of the latter two species show similar abundance patterns in the inter- and sub-tidal environments to those exhibited by *D. cervinus* and *S. durbanensis* i.e. they are more abundant intertidally in the eastern Cape and generally observed to be more abundant subtidally than intertidally throughout the Cape. It may therefore be concluded that they are not entirely dependent on rock-pools as nursery areas.

Conclusion

An analysis of the distribution and abundance patterns of the fish species found in Cape rock-pools has allowed an assessment of the importance of this habitat to the species that occupy it. Ninety-five per cent of the species commonly resident in the pools were endemic to southern Africa and they had an average distribution range of 1500 km. In contrast, only half the transient species were endemic, having an average distribution range of 2400 km, a considerably wider range than the residents even without the inclusion of the Indo-Pacific, circum-African and Atlantic species. These differences between the resident and transient groups may be attributed to their morphological and reproductive adaptations. The residents were all small, weak-swimming, demersal and cryptic species with limited dispersal phases for which long stretches of sandy coast are effective barriers to dispersal. These species, therefore, are adapted to conditions prevailing in limited areas where most are dependent on rock-pools throughout their lives. Most of the transients, on the other hand, were free-swimming species with pelagic eggs and larvae which can occupy considerably wider geographical areas.

The marked eastward increase in the number of species inhabiting the rock-pools was due not to the number of resident species, which remained similar throughout, but to an increase in the numbers of transient species present. This increase is largely a result of the proximity of the eastern Cape to the species-rich subtropical waters further north from which the southward transport of species is facilitated by the Agulhas current. Many of the species at the southern limits of their distribution in the eastern Cape are seldom found in the open sea and may rely on rock-pools for their southward extension because temperatures in this habitat are slightly elevated by the sun. Juveniles of most of the common transient species are, however, also found in adjacent shallow-water marine habitats. Species such as *Atherina breviceps, Diplodus sargus* and *Liza richardsoni* are abundant in the surf zone of sandy beaches, over shallow reef areas and in estuaries. These abundant, ubiquitous species also occur in pools at all shore levels and therefore appear to have the physiological capabilities to withstand a wide range of environmental conditions. Other transient species, for example *Sparodon durbanensis, Diplodus cervinus, Cheilodactylus fasciatus, Chirodactylus brachydactylus* and *Acanthistius sebastoides* have more specific habitat requirements; they are found only over inshore reefs and in large pools in the lower intertidal. The abundance of these species in rock-pools, is however, not great in comparison with their subtidal abundance and, when one considers the area of rock-pools available relative to the other habitats in which they occur, it may be safely concluded that Cape rock-pools do not serve an important nursery function for juvenile marine fish.

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CHAPTER 5.

The Fish Community of a Moderately Exposed Beach on the Southwestern Cape Coast of South Africa and an Assessment of this Habitat as a Nursery for Juvenile Fish

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The ichthyofauna of a moderately exposed surf-zone habitat on the southwestern Cape coast of South Africa was sampled by seine netting monthly for 13 months. Twenty species of fish, 40 306 individuals weighing a total of 211 kg were captured. The number of species and standing crop varied seasonally with higher values occurring during the summer (January–March). The average summer standing stock of 38·6 g m^{-2} was considerably higher than any previously recorded from a surf-zone habitat and the annual average (10·1 g m^{-2} was comparable with that in estuaries. Eighteen of the species sampled occurred almost exclusively as juveniles and only two as adults. Four species were present throughout the year, 11 of them seasonally and the remaining five sporadically. Small juveniles (20–35 mm) typically appeared in the surf-zone 2–4 months after they were spawned. These 0+ juveniles remained there for between three months and one year depending on species, before vacating the surf-zone for their adult habitats. A comparison of the abundance of juveniles in the surf-zone with other inshore marine habitats suggested that five species (*Amblyrhynchotes honckenii*, *Cheilodonichthys capensis*, *Diplodus sargus*, *Lithognathus mormyrus* and *Pomadasys olivaceum*) may be entirely, and three species (*Lichia amia*, *Liza richardsoni* and *Rhabdosargus globiceps*) largely, dependent on the surf-zone as a nursery area. It was concluded that the surf-zone of sandy beaches may be as important as estuaries as a nursery habitat for juvenile fish.

Introduction

The importance of estuaries and other sheltered coastal marine habitats as nursery areas for juveniles of many marine fish species is well-established in the literature and it has been shown that a large number of species are dependent on these areas during the juvenile phase of their life cycles (Gunter, 1967; Zijlstra, 1972; Jhingran & Gopalakrishnan, 1973; Lenanton, 1977; Poxton *et al.*, 1983; Warburton, 1979; Wallace *et al.*, 1984*a*). Typically, juvenile fish enter the nursery areas after metamorphosis having been spawned elsewhere in the sea. They remain in the nursery area for some time, often no more than a year, before vacating it for their adult habitat. This pattern of habitat utilization is considered to occur

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because sheltered habitats offer advantages over the marine environment in terms of protection from predators and an abundant food supply (Clark, 1974; Cushing, 1975; Lenanton, 1982; Boesch & Turner, 1984).

Fish communities of exposed sandy beaches are considerably less well-known, probably because this environment is difficult to sample effectively (Schaeffer, 1967). The studies that have been undertaken in this habitat have been concentrated primarily in the Gulf of Mexico (Gunter, 1958; McFarland, 1963; Modde, 1980; Modde & Ross, 1981; Ruple, 1984; Ross *et al.*, 1987) and, more recently, on the southeastern coast of South Africa (Lasiak, 1982, 1984*a*,*b*; Romer, 1986) and southwestern Australia (Lenanton, 1982; Lenanton *et al.*, 1982; Robertson & Lenanton, 1984). These studies have shown that the size and age structure of fish occupying sandy beaches, as well as their patterns of seasonal variation, are very similar to those found in estuaries. These similarities have led Lasiak (1981) and Lenanton (1982) to consider the possibility that the surf-zone of exposed sandy beaches may also act as a nursery area. They presented evidence to show that the surf-zone provides the requirements of increased food and shelter from predators necessary for it to function as a nursery area, but were unable to show that any species depended on this habitat as juveniles.

This report describes the species composition, standing crop, age structure and seasonal abundance of fish sampled in a moderately exposed sandy-beach surf-zone environment at Fishoek on the southwestern Cape coast of South Africa. These data are compared with studies elsewhere and with similar information from other inshore marine habitats in the southwestern Cape to provide an assessment of the importance of the surf-zone as a nursery habitat for juvenile marine fish.

Methods

The study site

Fishoek beach is situated at 34°08′S, 18°27′E on the eastern coast of the Cape Peninsula. It is 1·3 km long and is confined at its northern and southern ends by steep rocky shores. The gradient of the beach at its southern end where sampling was conducted was very flat (approximately 1:45) and fine sands predominated. The average wave height was 0·95 m which is representative of a medium energy beach (Heinecken, 1986). Sea temperatures during the winer months, when offshore winds prevail, were in the region of 15 °C. During summer, when winds are primarily onshore, they were approximately 20 °C. Salinities were 35·0–35·3% throughout the year (Atkins, 1970). Rooted aquatic macrophytes were absent but small drifts of finely fragmented detritus were occasionally evident.

Sampling

A seine net 25 m long, 2 m deep and with a stretched mesh size of 10 mm was used to sample the ichthyofauna of the surf-zone at Fishoek. The net was laid parallel to the beach 50 m offshore (in water approximately 1 m deep) by wading. It was hauled by six to eight persons, one at each end of the net and two to three others equidistantly placed along the two 30 m hauling ropes. Operated in this way the net swept an area of approximately 800 m^2. Two hauls approximately 100 m apart were made each month between May 1980 and May 1981. To standardize conditions, sampling always started at approximately 0830, between 12 and 36 h after the commencement of offshore winds following a period of onshore conditions. Monthly catches were combined, sorted by species, counted, measured to the nearest mm (TL) and each species batch-weighed. Standing stock was

calculated as catch (in numbers or g) per area sampled (800 m^2). Gonads of up to 30 fish per species were examined each month for signs of activity.

Species were subdivided into four groups according to their occurrence and the relative abundance of adults and juveniles throughout the year:

(1) Residents—species which were present in the surf-zone as adults and juveniles throughout the year;

(2) Juvenile migrants—species which were represented primarily by 0+ juveniles present either throughout the year or seasonally;

(3) Adult migrants—species which were present seasonally primarily as adults (1 + and older);

(4) Sporadics—species represented by few individuals which showed no seasonal pattern of occurrence.

The degree to which the species depend on the surf-zone as a nursery area was evaluated using similar criteria to those devised by Wallace *et al.* (1984*a*) for estuarine species, each species being allocated to one of five categories as follows:

(1) Species found almost exclusively in the surf-zone throughout their life cycles;

(2) Species whose juveniles occur almost exclusively in the surf-zone;

(3) Species whose juveniles occur mainly in the surf-zone but are also found in other habitats;

(4) Species whose juveniles occur in the surf-zone but are more abundant in other habitats;

(5) Species which occasionally stray into the surf-zone from other habitats.

Multivariate analyses were conducted using the techniques and transformations recommended by Field *et al.* (1982). Monthly samples were grouped using complementary classification and multidimensional scaling techniques, both of which were based on root-root transformed abundance data, together with the Bray-Curtis analysis of similarity.

Results

The fish community

Twenty species of fish representing 12 families totalling 40 306 individuals and weighing 211 kg, were caught during the 13-month sampling period (Table 1). Numerically *Atherina breviceps* (57·6%), *Lithognathus mormyrus* (23·1%) and *Liza richardsoni* (12·6%) dominated, providing 93·3% of the catch. The same three species were also most important in terms of biomass, together contributing over 95% of the total. A seasonal trend in the number of species was apparent, most (9–10) being caught between September and January and fewest (4–5) in April and May. The total number of fish in the monthly samples, however, merely reflected variations in the abundance of the dominant species named above. Multivariate analysis of the monthly samples separated them into three groups on the basis of similarities of their species composition and abundance (Figure 1). These groups correspond with the seasons: September to November (spring), December to March (summer), April to August (autumn and winter).

Four species, *L. mormyrus*, *Rhabdosargus globiceps*, *Diplodus sargus* and *L. richardsoni* were taken throughout the year and occurred in >80% of hauls. Small juvenile *L. mormyrus* and *R. globiceps* were caught in the surf-zone at lengths of <30 mm from May to July and December to June respectively. Both species were fully recruited into the catch by August after which time they increased in mean size, until, a year after recruiting and at

TABLE 1. The species composition and abundance of fish in two monthly seine net samples each of approximately 800 m² from the surf-zone of Fishoek beach

	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Total No.	Total mass (kg)
Atherinidae															
Atherina breviceps						29	5	152	274	19 770	3000			23230	168·84
Carangidae															
Lichia amia								2	4	7				13	0·34
Trachurus capensis					6		17							23	0·05
Clinidae															<0·005
Clinus latipennis								3						3	
Clupeidae															0·02
Gilchristella aestuaria					33									33	
Haemulidae															
Pomadasys olivaceum	121	116	279	8									74	598	0·28
Mugilidae															
Liza richardsoni	14	1433	527	1210	29	80	249	72	19	9	480	410	542	5074	25·52
Pomatomidae															
Pomatomus saltatrix								9	134	52	17			212	2·29
Sciaenidae															
Umbrina canariensis		2												2	0·01
Soleidae															
Heteromycteris capensis					2	3	2	1						8	0·01
Solea bleekeri						2								2	0·01
Sparidae															
Diplodus sargus	79	61	48	62	16	15	20	2	73		41	56	49	522	0·20
Lithognathus lithognathus						3								3	0·17
L. mormyrus	15	12	31	142	3258	1600	1760	157	43	1410	820	51	29	9328	8·55
Rhabdosargus globiceps	39	20	23	9	136	49	37	412	230	35	25	37	43	1095	4·23
R. holubi					2									2	0·01
Sarpa salpa							7							7	0·01
Sphyraenidae															
Sphyraena africana									1					1	0·03
Tetraodontidae															
Amblyrhynchotes honckenii							11	27	25	8				71	0·01
Triglidae															
Cheilodonichthys capensis		7	21	13	16	22								79	0·04
Total catch	268	1651	929	1444	3498	1803	2108	837	803	21 291	4383	554	737	40 306	210·62
Number of species	5	7	6	6	9	9	9	10	9	7	6	4	5	20	

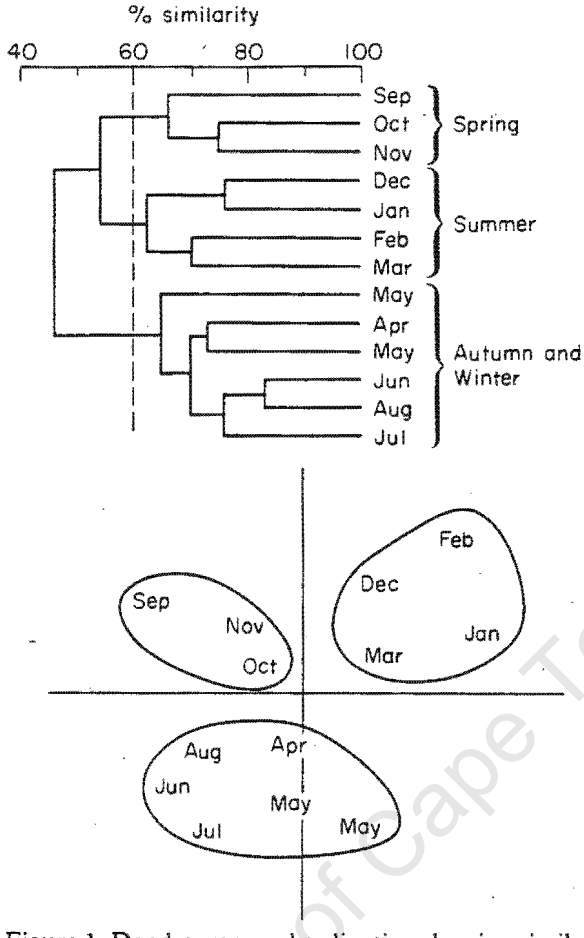

Figure 1. Dendrogram and ordination showing similarities between monthly seine net samples from the surf-zone of Fishoek beach.

lengths of approximately 80 mm, the cohorts had all but disappeared from the samples. The abundance of these two species increased after full recruitment to a maximum between September and February after which catches decreased as they apparently emigrated from the surf-zone.

Neither *L. richardsoni* nor *D. sargus* showed clear trends in mean size or abundance. The majority of *L. richardsoni* were 30–50 mm except for the period between November and January when larger specimens were taken. Almost all the *D. sargus* were 15–65 mm with individuals of < 25 mm being present from January to August and only larger individuals (35–65 mm) between September and December.

Seven species occurred seasonally, i.e. they were present for between three and six consecutive months and occurred in 15–35% of hauls. *A. breviceps, Pomatomus saltatrix, Amblyrhynchotes honckenii* and *Lichia amia* were present between November and February, *Pomadasys olivaceum* between May and August, *Cheilodonichthys capensis* between June and October and *Heteromycteris capensis* between September and December. The catch of all these species increased soon after they were first sampled in the surf-zone and, after reaching a peak, numbers declined probably as the combined result of natural mortality and emigration.

A further nine species were sampled, but together they provided only 0·19% of the total number of fish caught and occurred in $< 10\%$ of the hauls made (Table 1). These species do not merit individual attention as they occurred sporadically and in low numbers. It

is noteworthy, however, that eight of them were taken only between September and January.

Table 2 provides a summary of the information presented above and gives further facts about the reproduction and growth of the fish species sampled in the surf-zone. It also allows some important generalizations to be drawn about the utilization of the surf-zone by fish. All the fish sampled were small, the largest individual being 184 mm long, and all except two of the species (*A. breviceps* and *Gilchristella aestuaria*) were juveniles, most individuals being less than one year old. The 11 abundant and frequently occurring species were usually first sampled 2–4 months after spawning, at lengths of <50 mm. They remained in the surf-zone for three or more consecutive months during which time the cohorts of most species showed increments in mean length. Numbers sampled increased until the species was fully recruited into the catch and remained high for some time before decreasing through mortality and emigration from the surf-zone. Estimates of the relative abundance of adults and juveniles of species in the surf-zone and in adjacent marine habitats, drawn from various sources, are presented in Table 3. *L. richardsoni* was the only species abundant in the surf-zone as adults and juveniles and is therefore the only species that may be classified as a resident. Five other species were common or abundant in the surf-zone as juveniles. Three of them, *L. mormyrus, R. globiceps* and *D. sargus*, occurred throughout the year and two, *P. olivaceum* and *P. saltatrix*, occurred seasonally. Adults of these species were, however, rare or absent from the surf-zone and common elsewhere, and for this reason they were classified as juvenile migrants. Juveniles of four other species, *C. capensis, A. honckenii, L. amia* and *Trachurus capensis*, were considerably more common in the surf-zone than adults and for this reason were also classified as juvenile migrants. *A. breviceps* and *G. aestuaria* were only found as adults in the surf-zone. *A. breviceps* showed a clear seasonal pattern of occurrence, only adults being recorded in the surf-zone, and has its juvenile population centered in estuaries. It was therefore classified as an adult migrant. *G. aestuaria* and the remaining eight species listed in Table 3 were rare in the surf-zone and showed no pattern of occurrence and thus were classified as sporadics.

The data presented in Table 3 were also used to assess the degree to which juveniles depend on the surf-zone as a nursery area. Five species (*L. mormyrus, D. sargus, P. olivaceum, C. capensis* and *A. honckenii*) were allocated to category 2. All were common or abundant in the surf-zone and rare or absent from the other habitats for which information was available. An overwhelming majority of juveniles probably utilize the surf-zone as a nursery area and may therefore be entirely dependent on it during this phase of their life cycles. Category 3 species (*R. globiceps, L. richardsoni* and *L. amia*) were more abundant in the surf-zone as juveniles but they also occurred in other habitats and therefore are considered to be largely, but not entirely, dependent on the surf-zone nursery. Category 4 species occurred in the surf-zone in appreciable numbers but were relatively more abundant in other habitats, thus they benefit from the surf-zone nursery but are not dependent on it. Category 5 species are considered to be merely juvenile strays from other habitats and are in no way dependent on the surf-zone.

Discussion

Comparisons of the fish community at Fishoek with those studied elsewhere are complicated by a number of factors. Important among these is the type of sampling gear used. Variations in mesh size, foot rope weighting and the size of area swept by the net affects the

TABLE 2. Summary of information on the occurrence, size, reproduction and recruitment of fish species occupying the surf zone of Fishoek beach. Blank spaces indicate data are not available, not relevant or unreliable because of small sample sizes. All lengths are in mm total length

	% Occurrence	Length range	Length at maturity	% Juveniles	Length at 1 yr old	% < 1 yr old	Spawning period	Recruitment period	Length at recruitment	Season of peak abundance
Amblyrhynchotes honckenii	15	17–33						Nov–Dec	< 20	Summer
Atherina breviceps	35	64–136	43[a]	0	60[a]	0	Sept–Nov[f]	Dec–Feb	60–140	Summer
Cheilodonichthys capensis	27	21–52	320[b]	100	105[b]	100	Sept–Mar[b]	Jun–Jul	< 25	Winter/spring
Clinus latipennis	4	26–33								
Diplodus sargus	81	19–74	150[c]	100			All year[c]	Jan–Aug	< 35	All year
Gilchristella aestuaria	4	41–53	34[a]	0						
Heteromycteris capensis	19	31–57					All year[n]	Sept–Nov	< 50	Spring
Lichia amia	23	67–135	550[d]	100	220[j]	100	Aug–Oct[o]	Nov–Dec	70–120	Summer
Lithognathus lithognathus	4	146–184	500[e]	100	140[e]	50	Jul–Aug[e]			
L. mormyrus	96	18–89		100	72[n]	86	Dec–Feb[n]	May–July	< 30	Spring
Liza richardsoni	89	20–18	250[d]	100	120[j]	100	Sept–Mar[p]	All year	< 50	All year
Pomadasys olivaceum	35	20–52	130[f]	100			Nov–Mar[n]	May	< 30	Winter
Pomatomus saltatrix	23	47–158	280[f]	100	170[f]	100	Sept–Nov[f]	Dec–Feb	60–140	Summer
Rhabdosargus globiceps	92	14–109	260[d]	100	80[n]	80	Oct–Feb[q]	Dec–Jan	< 30	Spring/summer
R. holubi	4	64–67	180[d]	100	60[i]	0	May–Aug[d]			
Sarpa salpa	4	33–46	170[g]	100	90[k]	100	Jun–Sep[g]			
Solea bleekeri	4	47–59	100[h]	100			Jun–Aug[h]			
Sphyraena africana	4	155								
Trachurus capensis	8	33–49		100	83[l]	100	July–Sept[l]			
Umbrina canariensis	4	45–60								

[a]Bennett (in press); [b]Hecht (1977); [c]Coetzee (1986); [d]Day *et al.* (1981); [e]Mehl (1973); [f]van der Elst (1976); [g]Joubert (1981); [h]Wallace (1975); [i]Blaber (1974); [j]Ratte (1976); [k]Lasiak (1983*a*); [l]Geldenhuys (1973); [m]Smith & Smith (1986); [n]Lasiak (1982); [o]van der Elst (1981); [p]Lasiak (1983*b*); [q]Talbot (1955).

TABLE 3. The relative abundance of adults and juveniles of fish species sampled in the surf zone at Fishoek beach as well as in estuaries, inshore areas of sandy substrata (10–50 m depth), shallow reefs (2–25 m) and intertidal rock pools in the southwestern Cape. **** indicates that adults or juveniles constituted >5% of the total numerical abundance observed in that habitat, *** >0·5%, <5%, ** >0·05% <0·5% and * <0·05%. See text for explanations of nursery categories 2–5 which represent progressively decreasing juvenile association with surf-zone.

	0+ Juveniles					Adults (in >1 yr old)					
	Surf zone	Estuaries	Inshore sandy	Reefs	Rock pools	Surf zone	Estuaries	Inshore sandy	Reefs	Rock pools	Nursery dep.
Data sources	*a*	*b,c*	*d*	*e,b,g*	*h*	*a,b,g,i*	*b,c*	*d*	*e,b,g*	*e,h*	
Residents											
Liza richardsoni	****	****		*	*	****	***		*		3
Juvenile migrants											
Amblyrhynchotes honckenii	**					*	*	*	*		2
Cheilodonichthys capensis	**							**			2
Diplodus sargus	***	*		*	*	*	*		**		2
Lichia amia	**	**				*	**				3
Lithognathus mormyrus	****		*			*	*	****	*		2
Pomadasys olivaceum	***		*					****	*		2
Pomatomus saltatrix	***	**	****			*	*	***	*		4
Rhabdosargus globiceps	***	***		*		*	*	**	**		3
Trachurus capensis	**	*	***					***	*		4
Adult migrants											
Atherina breviceps		****				****			*	*	5
Sporadics											
Clinus latipennis	*								*		5
Gilchristella aestuaria		****				**	****				5
Heteromycteris capensis	*	*					*				4
Lithognathus lithognathus		***				*	*		*		5
Rhabdosargus holubi		**				*	*		*		5
Sarpa salpa	*			**			*		****		5
Solea bleekeri	*	*						**			4
Sphyraena africana	*										5
Umbrina canariensis	*		*					*	*		4

[a]This paper; [b]Bennett (in press); [c]Bennett *et al.* (1985); [d]Wallace *et al.* (1984*b*); [e]Bennett (unpublished); [f]Day *et al.* (1970); [g]Penrith (1976); [h]Bennett & Griffiths (1984); [i]De Villiers (1976).

size and species composition of the catch which, in turn, affects age composition, density and standing stock. The range of conditions under which sampling is conducted is also important since it has been shown that the ichthyofauna at a particular locality may change with such factors as time of day or night, tides, sea state and wind (Lasiak, 1984*a*; Ross *et al.*, 1987). Escapement from the gear used in this study is unknown; flatfish and burrowing species were almost certainly underestimated but free swimming ' roundfish ' of between 20–30 mm and approximately 150 mm are considered to have been sampled reasonably effectively. The range for the lower limit of selectivity depends on the cross sectional area of the individual species. Thus ' broad ' species such as *A. honckenii* and *C. capensis* were fully recruited at a smaller size than elongate species like *L. richardsoni*. The upper limit is the ability of large fish to escape from the area being swept while the net is laid. Larger *L. richardsoni* were the only fish observed escaping the net in this way, thus the results presented here are considered representative for all other species large enough to be retained by the mesh used. Variability of catch composition due to changes in physical conditions was minimized by restricting sampling to a fixed time of day and similar stages in the wind cycle. Limitations such as these should be borne in mind when comparisons are made between surf-zone ichthyofaunas.

Notwithstanding possible differences in sampling technique, the average standing stock and density of fishes recorded at Fishoek is clearly high relative to that of most comparable studies elsewhere. Ross *et al.* (1987) tabulated literature values for average standing stocks obtained in temperate-subtropical inshore marine environments obtained during the three month period of maximum abundance. Their values ranged from 0·8 to 57 g m^{-2} with the high values resulting from drop net and rotenone samples and lows from seines and trawls. The standing stock obtained at Fishoek between January and March, when it was at a maximum, was 38·6 g m^{-2}. This value is exceeded only by the drop net samples of Hellier (1962) in the Laguna Madre and the rotenone samples of Perry (1976, cited by Ross *et al.*, 1987) in a Louisiana estuarine area. It is considerably higher than the 11·9 g m^{-1} recorded by McFarland (1963) which was the highest standing crop previously recorded by seining in a surf-zone. In fact, McFarland's (1963) figure is comparable with the annual average (10·1 g m^{-1}) at Fishoek.

Reasons for the high standing crop at Fishoek are unknown but one species, *A. breviceps* was predominant (80% mass and 58% numbers). The dominance of surf-zone ichthyofaunas by one or a few species has been noted previously (Lasiak, 1984*b*; Ross *et al.*, 1987) but in most cases approximately 90% of the catch was provided by 5–10 species. It is only in the catches of Romer (1986), who used a 50 mm mesh net to sample an exposed beach on the southeastern coast of South Africa, that one species (*L. richardsoni* 90% mass, 93% numbers) exceeded the contribution of *A. breviceps* at Fishoek.

The magnitude of seasonal variations in the ichthyofaunas of exposed beaches that have been reported differ quite markedly. In the northern Gulf of Mexico fish are virtually absent from the surf-zone during the winter months (Gunter, 1958; McFarland, 1963; Modde, 1980; Ross *et al.*, 1987), whereas in southwestern Australia some species occur year-round and some are seasonal (Lenanton, 1982). In other areas, such as on the south-eastern coast of South Africa, there is very little variation in the number of species or abundance through the year, although variation amongst individual species has been noted (Lasiak, 1984*b*). At Fishoek only half the maximum number of species was present during the winter months but total abundance reflected the abundance patterns of the dominant species, some of which were present throughout the year and others during different seasons. Differences in the strength of seasonal cycles that have been reported

therefore appear to reflect the magnitude of seasonal variation in physical conditions, of which water temperature is probably the most important, and are thus primarily governed by latitude.

Half the species sampled at Fishoek were classified as juvenile migrants, eight as sporadics and one species each as adult migrants and residents. A predominance of juveniles in samples from exposed surf-zones has been observed by Lasiak (1984*a*), Modde and Ross (1981), McDermott (1983) and Robertson and Lenanton (1984), and a general pattern of seasonal occurrence was recorded by a number of authors including Warfel and Merriman (1944), Modde (1980) and Lenanton (1982). Classification of the species has, however, resulted in some confusion because, although resident and migrant categories have been widely recognized, differences in the criteria used to categorize the species have resulted in species with similar patterns of surf-zone utilization being classified differently. The most common pattern observed at Fishoek was that species were first sampled approximately 2–4 months after spawning and remained either for a season or during their first year of life before departing to some other habitat. These species were considered to be migrants because, although they resided in the surf-zone for some period, the remainder of their life cycle was completed elsewhere.

The nursery function of an exposed surf-zone habitat has been investigated by Lasiak (1981, 1986) who showed it to be relatively predator-free and food-rich, but stopped short of suggesting that any species depended on it as a nursery area. If the criteria used by Wallace *et al.* (1984*a*) to signify estuarine dependence are applicable to the surf-zone, then the results presented in this paper suggest that a number of species depend on it as a nursery area. Of the species sampled at Fishoek five were considered more abundant in the surf-zone, and three at least as abundant there as in other inshore habitats. This means that eight of the nine juvenile migrants may be considered wholly or largely dependent on the surf-zone as a nursery area. When almost identical criteria were used to assess juvenile dependence on estuaries in the southwestern Cape (Bennett, in press), it was found that five of the eleven juvenile migrants frequenting these estuaries are entirely and three largely dependent on them as nursery areas. These results indicate that the surf-zone of sandy beaches on the southwestern Cape coast of South Africa are as important as estuaries as a nursery area for juvenile migrant species. This finding is supported by the fact that the average standing stock and density in the surf-zone sampled (10·1 g m^{-2}, 1·94 fish m^{-2}) is very similar to that found by Bennett (in press) in estuaries (11·7 g m^{-2}, 2·1 fish m^{-2}) in the same area. Further, when one considers that the area of surf-zone available in the southwestern Cape is large relative to that of estuaries, it is reasonable to assume that a greater number of fish are dependent on the surf-zone nursery.

A. breviceps was the only adult migrant species sampled during this study. Gonads of nearly all individuals examined were ripe, indicating that spawning was imminent, and an examination of stomachs suggested that they were actively feeding while in the surf-zone. The species may therefore have migrated into the surf-zone either to spawn or because better feeding conditions were available there. There is, however, no evidence to support either possibility. A further explanation of their presence in the surf-zone during the summer months may be that they were attempting to escape summer migrant predators such as *P. saltatrix*, *Argyrosomus hololepidotus* and *Seriola lalandii* which frequent inshore waters in the southwestern Cape at this time (unpublished records of the Sea Fisheries Research Institute, Cape Town). Although the samples on which this report is based are considered representative of small fish at Fishoek under a particular set of conditions, large fish were not adequately sampled and, with the exception of *A. breviceps*, data on

surf-zone utilization by adults are lacking. Personal observations of the catches of commercial seine net fisherman and surf anglers reveal that larger individuals of a number of species do enter the surf-zone, often in very large numbers. These fish are, however, usually taken in slightly deeper water and during weather and sea conditions that were not sampled in this study. An investigation of these species, which may form a discrete group of major importance among the surf-zone ichthyofauna, remains a priority for the future.

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CHAPTER 6.

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A COMPARISON OF THE FISH COMMUNITIES IN NEARBY PERMANENTLY OPEN, SEASONALLY OPEN AND NORMALLY CLOSED ESTUARIES IN THE SOUTH-WESTERN CAPE, SOUTH AFRICA

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Seine-netting for 13 consecutive months in the permanently open Palmiet Estuary, in the seasonally open Kleinmond Estuary, and in the Bot Estuary, which had been closed for three years, yielded 101 000 fish. Seven species complete their entire life cycles in estuaries, 13 breed in the sea and migrate into the estuaries as juveniles, and two were freshwater species. Classification and ordination showed that the structure of the communities changed markedly during heavy freshwater flushing in the Palmiet and Kleinmond estuaries but not in the Bot. This was related to a massive emigration of species and individuals in the former two systems. Spawning by the permanent residents in spring/summer ensures minimal loss of eggs and larvae from the estuaries and allows juveniles to benefit from favourable summer and autumn conditions. Winter spawning by the marine migrants allows juveniles to enter the estuaries in the spring and early summer, after the winter floods but before the estuaries close. Differences in the species composition of the three estuaries are related to differences in the duration of connection between the estuaries and the sea.

Seënvangste oor 13 opeenvolgende maande in die permanent oop Palmietgetymonding, in die seisoenmatig oop Kleinmondgetymonding en in die Botgetymonding, wat vir drie jaar toe was, het 101 000 visse opgelewer. Sewe spesies voltooi hul lewensloop in getymondings, 13 broei in die see en migreer na getymondings as jongvis en twee was varswaterspesies. Klassifikasie en rangskikking het aangetoon dat die struktuur van die gemeenskappe aansienlik tydens sterk varswaterspoeling in die Palmiet- en die Kleinmondgetymonding verander het maar nie in dié van die Botrivier nie. Dit het verband gehou met 'n massale emigrasie van spesies en individue by die eersgenoemde twee stelsels. Deurdat die vaste inwoners in die lente/somer kuitskiet, word verseker dat die verlies aan eiers en larwes uit die getymondings minimaal is en word jongvis toegelaat om te baat by die gunstige somer- en herfstoestande. Deurdat die mariene migreerders in die winter kuitskiet, word hul jongvis in staat gestel om die getymondings in die lente en vroegsomer binne te kom, na die wintervloede maar voor die getymondings toegaan. Die verskille tussen die spesiesamestelling van die drie getymondings hou verband met hoe lank die verbinding tussen 'n getymonding en die see voortduur.

The species composition, abundance and size distribution of the fish fauna of temperate estuaries typically undergo seasonal variations. Generally, fewer species and individuals are present during winter and abundance and species diversity increase during spring to reach a peak in summer/autumn. The species primarily responsible for these seasonal trends breed in the sea and migrate into the estuaries as small juveniles where they remain, usually for less than a year, before migrating back to the sea (Gunter 1938; Dahlberg and Odum 1970, Oviatt and Nixon 1973, Cain and Dean 1976, Whitfield 1980, Horn and Allen 1981, Marais 1981, Beckley 1984, Claridge *et al.* 1986). Because estuaries are highly productive and usually have shallow, calm, turbid waters, they offer juvenile fish good conditions for growth and protection from predators. Such conditions are frequently less suitable for juveniles in adjacent marine environments (Clark 1974, Cushing 1975, Wallace and van der Elst 1975, Blaber and Blaber 1980, Lasiak 1981, Lenanton 1982, Boesch and Turner 1984). Indeed, many species of fish are said to be dependent on estuaries during the juvenile phase of their life cycles (Wallace *et al.* 1984).

There is a marked tendency for bars to form at the mouths of many estuaries in southern Africa (Day 1951). While some blind estuaries are often breached each winter or spring when freshwater discharge peaks, others may remain closed from the sea for periods of one or more years. Their formation influences patterns of recruitment of marine species and thereby also the composition of the fish fauna in the estuary.

The aim of the present study was to compare the composition and seasonal changes in the structure of the fish fauna of a permanently open estuary (Palmiet) with one which is seasonally closed (Kleinmond) and with another that was closed for three years (Bot).

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METHODS

Monthly samples were obtained by seine net from three sites in the Bot Estuary and two sites in each of the Kleinmond and Palmiet estuaries (Fig. 1). Both of the two 12,5 m wings of the seine were attached to 30-m long ropes, which were used to haul the net onto the beach after it had been laid parallel to the shore. The net, which consisted of 10-mm stretched mesh, sampled to a depth of 1,5 m and covered an area of 525 m². Two hauls were made in adjacent areas at each site between April 1980 and April 1981, except in those cases where it was only feasible to perform a single haul. Monthly catches from within each estuary were pooled, sorted into species and counted. The total length (*TL*) of each fish was measured to the nearest 1 mm, except where numbers were large, in which case measurements were restricted to a sub-sample of 200. The total weight and the number of the catch of each species was expressed as catch per haul. Gonads of up to 75 fish of each species were examined monthly and, from the criteria listed in Table I, categorized as immature/inactive, active or ripe. The length at 50-per-cent maturity was taken as the length at which half the fish sampled had active or ripe gonads during the breeding season.

For analysis of modal progression, the length distributions were grouped into the smallest intervals at which clear modes could be identified and followed. Conclusions are then drawn on age classes. Although other modes may have been hidden in the selected groupings by length for each species and, though no back-up age determination (of, for instance, otoliths) was carried out or could be found in the literature, the conclusions are confidently predicted to be as accurate as the data allow. The data on numbers for each month in each of the three estuaries were transformed and subjected to classification and multidimensional scaling (MDS), following the procedures described by Field *et al.* (1982).

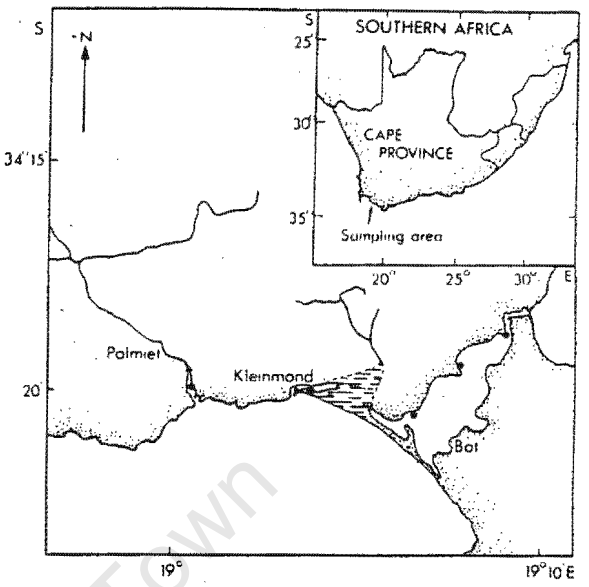

Fig. 1: Map of southern Africa (inset) and the location of the sampling sites in the three estuaries

RESULTS

Study area

The South-Western Cape (32–35°S, 18–20°E, Fig. 1) has a Mediterranean-type climate with hot, dry and windy summers and cooler, wetter winters. The mean annual temperature is approximately

Table I: Criteria used for allocating gonads to reproductive stages

	Immature/Inactive	Active	Ripe
Females	Gonads small (extending < 25% of body cavity), no ova or embryos visible	Gonads enlarged (25–40% of body cavity), eggs visible (±0,4–0,7 mm diameter). *Clinus spatulatus*: embryos < 10 mm present	Ovaries extend for > 50% of body cavity. Eggs visible and easily freed from surrounding tissue. Superficial blood vessels evident. *C. spatulatus*: embryos > 10 mm present
Males	Gonads threadlike, no milt present	Gonads enlarged (at least double diameter of previous stage), some milt may be extruded under pressure	Testes considerably enlarged, milt easily extruded. *Syngnathus acus* carrying eggs or larvae in brood pouch

17°C, with monthly means ranging from 21°C in January to 13°C in July. Mean annual rainfall in the region is 700 mm, with the highest and lowest rainfall falling in July (c. 100 mm) and February (c. 15 mm) respectively (Heydorn and Tinley 1980).

The characteristics of the catchments and basins of the three estuaries differ markedly. The susceptibility to flooding and the duration and frequency with which their mouths are open to the sea also varies. As the Palmiet Estuary is small (0,25 km²), channel-like and receives a continuous run-off from a mountainous catchment ($310 \times 10^6 m^3 \cdot year^{-1}$), the mouth apparently remains open. Sediments are coarse and the only submerged macrophyte present is *Cladophora*, sparse growths of which become established in late summer when river flow is at a minimum (Branch and Day 1984).

While the Bot Estuary, with a surface area of 23 km² when full, is larger than the Palmiet, it receives only about one-third of the freshwater discharge. Such a relatively low input, and the fact that the estuary has a natural "spillway" which allows overflow to Kleinmond when water levels are high, means that the mouth is rarely breached naturally (Branch *et al.* 1985). At the time sampling commenced, the estuary had not been in contact with the sea for 32 months, with the result that water levels were high and aquatic macrophytes, primarily species of *Ruppia*, *Potamogeton*, *Chara* and *Cladophora*, had become well established. The water level in the estuary increased by 0,7 m between April and August 1980 and remained at this level until November. Although levels subsequently declined briefly, they remained far above those recorded in years when the bar was opened artificially (Bally and McQuaid 1985). Unseasonal heavy rains in late December and early January 1981 caused water levels to rise above "spillway" level, and "overflowing" occurred until the end of February.

The size, duration of connection with the sea and the severity of flooding of the Kleinmond Estuary is intermediate between those of the Bot and Palmiet estuaries. During the first four months of sampling, the mouth was closed and the estuary densely vegetated by *Cladophora*. The water level was relatively constant during April and May but increased in June. By July, freshwater discharge had reached levels which resulted in the bar becoming breached, and the sudden strong outflow to the sea resulted in the water level dropping by approximately 2 m. While most of the weed was flushed out to the sea, some became stranded along the estuary. Continued flooding scoured the estuary and kept temperatures and salinity low. At the onset of the dry season, longshore drift began to close off the mouth, water

Table II: Species composition and abundance in monthly seine-net samples from the Palmiet Estuary

Species	Class*	Catch per haul														% numbers	Total mass (kg)
		Apr. 1980	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Jan. 1981	Feb.	Mar.	Apr.	All months		
Liza richardsoni	T	31,0	1 153,5	381,0	295,0	72,5	307,0	54,0	8,0	325,5	218,0	1 329,0	145,5	267,0	4 587,0	49,7	44,17
Atherina breviceps	R	3,0	3 900,0				33,5	2,0		5,0				44,0	3 987,5	43,2	1,53
Psammogobius knysnaensis	R	11,5	23,0	25,5	35,0	4,5	6,5	13,0	3,5	3,0	8,0	70,5	31,0	15,5	250,5	2,7	0,10
Lithognathus lithognathus	T	5,0						11,0	24,5	64,5	7,0	64,5	14,5	3,5	194,5	2,1	3,51
Liza dumerili	T	34,0	6,5											25,5	66,0	0,7	0,04
Myxus capensis	T	11,5	9,0				4,0	0,5	3,5	3,5	0,5		7,0	4,5	44,0	0,5	0,39
Gilchristella aestuaria	R								4,5		4,5	25,5	4,0		38,5	0,4	0,01
Rhabdosargus holubi	T	1,0								1,5	0,5	5,5	5,0	3,5	17,0	0,2	0,11
Rhabdosargus globiceps	T	4,5							1,5	2,5	1,0	2,5	1,5	2,0	15,5	0,2	0,24
Mugil cephalus	T	1,5						1,0	2,5				0,5	2,5	8,0	0,1	0,19
Caffrogobius multifasciatus	R						0,5	2,0				0,5	1,5	1,0	5,5	0,1	0,01
Pomatomus saltatrix	T									1,5	1,0				2,5	<0,05	0,01
Lichia amia	T									1,0	0,5	0,5	0,5		2,5	<0,05	0,19
Solea bleekeri	T								0,5		0,5		0,5		1,5	<0,05	<0,005
Liza tricuspidens	T											0,5			0,5	<0,05	0,01
Total		103	5 092	407	330	77	352	84	49	408	241	1 499	211	369	9 221		50,52
Number of species		9	5	2	2	2	5	7	8	9	10	9	11	10	15		

* T = Transient species
R = Resident species

levels rose and *Cladophora* became re-established. The mouth was intermittently closed between November and February and was then closed permanently until the end of the study in April 1981.

Fish populations

PALMIET ESTUARY

A total of 18 442 fish weighing 101 kg and representing 15 species was caught during the 13-month sampling period (Table II). In terms of abundance, the catch consisted almost entirely of *Lisa richardsoni* (50%) and *Atherina breviceps* (43%). Only two other species, *Psammogobius knysnaensis* (2,7%) and *Lithognathus lithognathus* (2,1%) contributed more than 1 per cent to the total catch. The species with the highest frequency of occurrence in samples taken from the separate sites in each month were *L. richardsoni* (100%), *P. knysnaensis* (88%), *Myxus capensis* (50%) and *L. lithognathus* (46%). The total number of species caught monthly decreased from nine in April 1980 to two between June and August. The number of species began to increase after the cessation of the winter rains in August, and culminated in a maximum of 11 species in March 1981 (Fig. 2).

Classification grouped the fish samples separately from winter (June–September), summer (October–February) and autumn (March and April). The May sample was grouped with those of winter, but at a lower level of similarity (Fig. 3). The same trends were observed after MDS ordination.

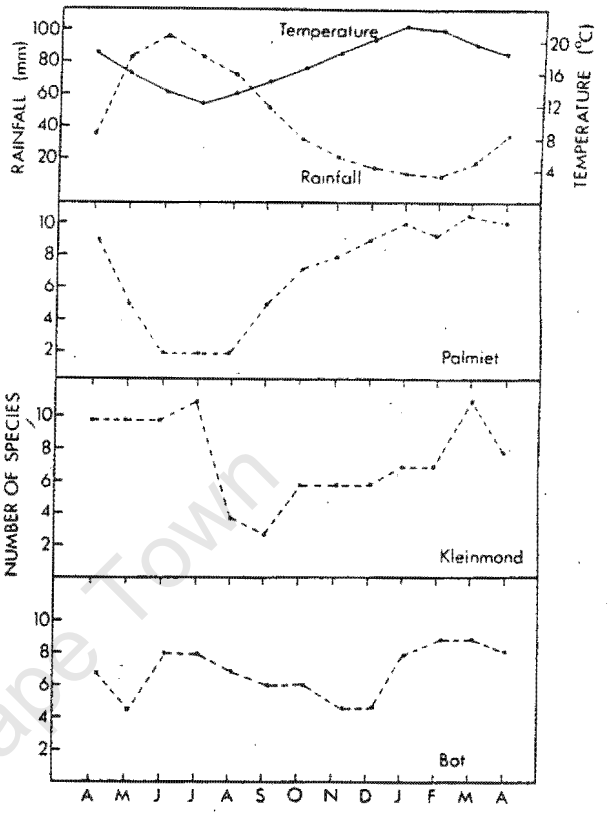

Fig. 2: Monthly rainfall and temperature data for Cape Town (from Heydorn and Tinley 1980) and seasonal changes in the number of species sampled in the Palmiet, Kleinmond and Bot estuaries

KLEINMOND ESTUARY

A total of 38 000 fish weighing 183 kg and representing 18 species was caught in the Kleinmond Estuary (Table III). *Atherina breviceps* contributed 77,9 per cent of the total catch. *Liza richardsoni* (14,3%), *Mugil cephalus* (1,1%), *Psammogobius knysnaensis* (2,6%) and *Lithognathus lithognathus* (2,4%) were the only other species to contribute more than 1 per cent. The five species occurring in over half the hauls were *A. breviceps* (100%), *L. richardsoni* (94%), *P. knysnaensis* (64%) and *Rhabdosargus holubi* (52%). Most species (10–11) were caught between April and July when the mouth was closed, numbers decreasing rapidly after opening to four in August and three in September. Thereafter, numbers increased again to the maximum of 11 species in March 1981 (Fig. 2).

Classification and MDS ordination separated the monthly fish samples into three groups, April–July 1980, August–October 1980 and November 1980–April 1981 (Fig. 4).

BOT ESTUARY

Some 45 000 fish weighing a total of 62,2 kg and representing 14 species were caught during the sampling period (Table IV). In terms of numbers, the total catch taken over the 13 months was also dominated by *Atherina breviceps* (78,7%). Together with *Gilchristella aestuaria* (16,0%), *Psammogobius knysnaensis* (2,3%) and *Clinus spatulatus* (1,5%), these species contributed virtually the total catch. The same four species also occurred most frequently in the different samples. Thus, *Atherina breviceps* was taken in every haul, *C. spatulatus* in 82 per cent

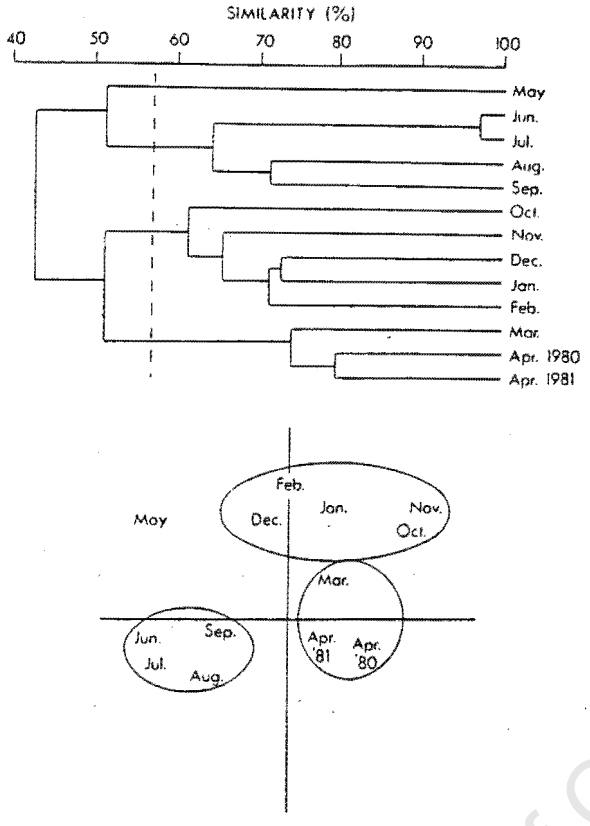

Fig. 3: Dendrogram and ordination showing similarities between monthly seine-net samples from the Palmiet Estuary

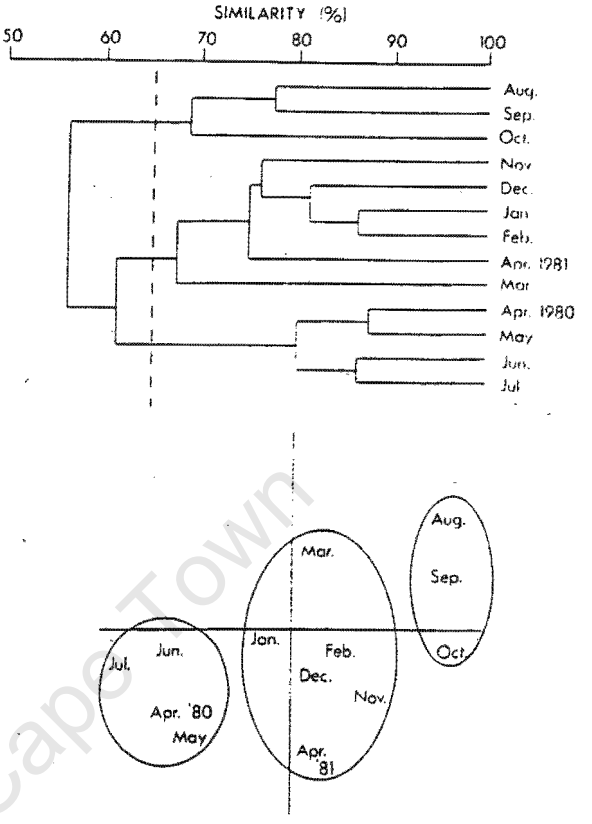

Fig. 4: Dendrogram and ordination showing similarities between monthly seine-net samples from the Kleinmond Estuary

of hauls, *P. knysnaensis* in 77 per cent and *G. aestuarius* in 72 per cent. The number of species, which ranged only from five to nine, showed no obvious seasonal trends (Fig. 2). The slightly greater numbers of species recorded during June and July and between January and March can be attributed to the effects of increased riverine input during those months. During these periods the normally freshwater species *Oreochromis mossambicus* and *Cyprinus carpio* expanded their ranges into the estuary. Moreover, the presence of water in the overflow channel to the Kleinmond Estuary for a brief period between late December and early January allowed juvenile *Liza richardsoni* to enter the Bot from the neighbouring Kleinmond Estuary.

Classification and ordination separated the fish samples from the Bot Estuary into two main groups, the first consisting of those taken in May, July and December and the second of those obtained in all other months (Fig. 5).

Utilization of estuaries by marine species

A comparison of the numbers and sizes of the various species in the Palmiet and Kleinmond estuaries with those in the Bot Estuary provided strong evidence that all of the 13 species listed in Table V are marine teleosts which, in the Western Cape, use estuaries as nursery areas. Therefore, while small juveniles of all these species were caught in abundance in the Palmiet and Kleinmond estuaries, which were open for at least part of the year to the sea, none were taken in the Bot which, unlike the other two estuaries, had been closed from the sea for the previous 32 months. The only exception to this

Table III: Species composition and abundance in monthly seine-net samples from the Kleinmond Estuary

Species	Class*	Catch per haul												All months	% numbers	Total mass (kg)
		Apr. 1980	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Jan. 1981	Feb.	Mar.	Apr.			
Atherina breviceps	R	423,0	537,3	143,0	1 693,0	2 350,0	1 830,5	230,5	590,0	612,5	430,0	850,0	2 880,5	230,0	12 800,3	77,9	10,38
Liza richardsoni	T	17,0	24,3	11,7	125,5	45,5	560,0	133,0	108,5	133,0	578,5	300,0	296,5	25,0	2 358,5	14,3	23,36
Psammogobius knysnaensis	R	19,5	23,0	15,0	12,5	32,0	14,5	6,5	202,5	8,5	17,5	39,0	6,0	27,5	424,0	2,6	0,38
Lithognathus lithognathus	T	38,5	27,8	95,3	135,0				11,0	14,5	33,5	24,5	4,5	9,0	393,6	2,4	12,89
Mugil cephalus	T	8,5		23,0	54,0	84,5		6,0					4,0		180,0	1,1	20,12
Rhabdosargus holubi	T	23,5	14,8	50,3	11,0			1,0	1,5	1,0	3,0		4,0	2,5	112,6	0,7	4,89
Oreochromis mossambicus	F	22,0	43,3	3,3	22,0										90,6	0,6	0,76
Rhabdosargus globiceps	T	0,5		0,7	15,5					0,5	6,0	4,5	9,5	4,0	41,2	0,3	0,72
Lichia amia	T	1,0	2,5	0,7	1,0							2,0	1,0		8,2	<0,05	2,78
Caffrogobius multifasciatus	R	0,7	0,5		0,5			3,5	2,0						7,4	<0,05	2,72
Gilchristella aestuaria	R										3,0	1,5		1,0	5,5	<0,05	0,03
Sarpa salpa	T												5,0		5,0	<0,05	<0,005
Myxus capensis	T													4,0	4,0	<0,05	0,05
Pomatomus saltatrix	T												3,5		3,5	<0,05	0,09
Diplodus sargus	T		0,3										0,5		0,8	<0,05	0,05
Liza tricuspidens	T				0,5										0,5	<0,05	0,01
Clinus spatulatus	R		0,3												0,3	<0,05	0,01
Syngnathus acus	R			0,2											0,2	<0,05	0,01
Total		554	674	343	2 071	2 512	2 405	381	916	770	1 072	1 222	3 215	303	16 437		79,23
Number of species		10	10	11	14	4	3	6	6	6	7	7	11	8	18		

* T = Transient species
R = Resident species
F = Freshwater species

Table IV: Species composition and abundance in monthly seine-net samples from the Bot Estuary

Species	Class*	Catch per haul													All months	% numbers	Total mass (kg)
		Apr. 1980	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Jan. 1981	Feb.	Mar.	Apr.			
Atherina breviceps	R	323,0	227,7	150,3	190,7	317,7	467,0	1 400,0	1 033,3	933,7	3 400,0	1 233,7	1 533,7	495,3	11 706,1	78,7	8,52
Gilchristella aestuaria	R	55,7		404,3		37,7	481,7	198,3	59,0		88,7	196,0	655,7	208,7	2 385,8	16,0	0,53
Psammogobius knysnaensis	R	14,0	0,7	10,3	0,3	7,3	8,3	48,0	54,3	7,3	53,3	3,7	104,0	33,3	344,8	2,3	0,23
Clinus spatulatus	R	2,7	5,3	2,0	8,0	12,7	22,3	13,7	133,0	8,0	2,3	2,7	6,0	11,7	230,4	1,5	0,50
Liza richardsoni	T			2,3	1,0						3,7	71,3	31,3	18,0	127,6	0,9	0,60
Syngnathus acus	R	10,0	5,3		15,3	1,0	1,3	2,3	2,0	2,7	2,3	1,0	8,3	1,3	52,8	0,4	0,02
Caffrogobius multi-fasciatus	R	6,7	0,3	1,7	0,7		0,3			2,0	0,3		4,3	1,3	17,6	0,1	0,07
Lithognathus lithognathus	T				5,0							3,0			8,0	0,1	8,10
Mugil cephalus	T			2,7		0,3							0,3		3,3	<0,05	1,15
Hyporhamphus capensis	R							0,3			1,7				2,0	<0,05	0,01
Cyprinus carpio	F											0,3	0,7	0,3	1,3	<0,05	0,55
Lichia amia	T					1,0									1,0	<0,05	0,38
Oreochromis mossambicus	F			0,3	0,3							0,3			0,9	<0,05	<0,005
Rhabdosargus holubi	T	0,3													0,3	<0,05	<0,005
Total		412	239	574	221	378	981	1 663	1 282	954	3 552	1 512	2 344	770	14 882		20,73
Number of species		7	5	8	8	7	6	6	5	5	8	9	9	8	14		

* T = Transient species
R = Resident species
F = Freshwater species

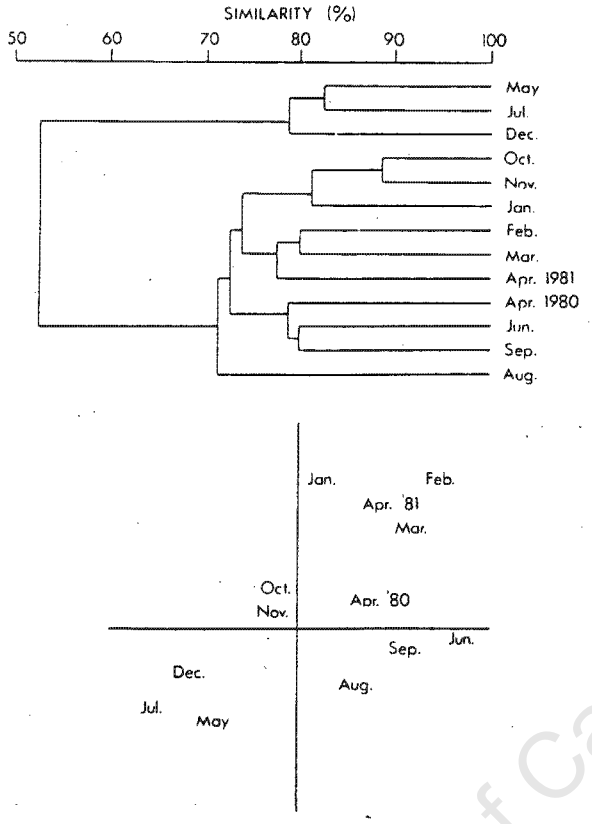

Fig. 5: Dendrogram and ordination showing similarities between monthly seine-net samples from the Bot Estuary

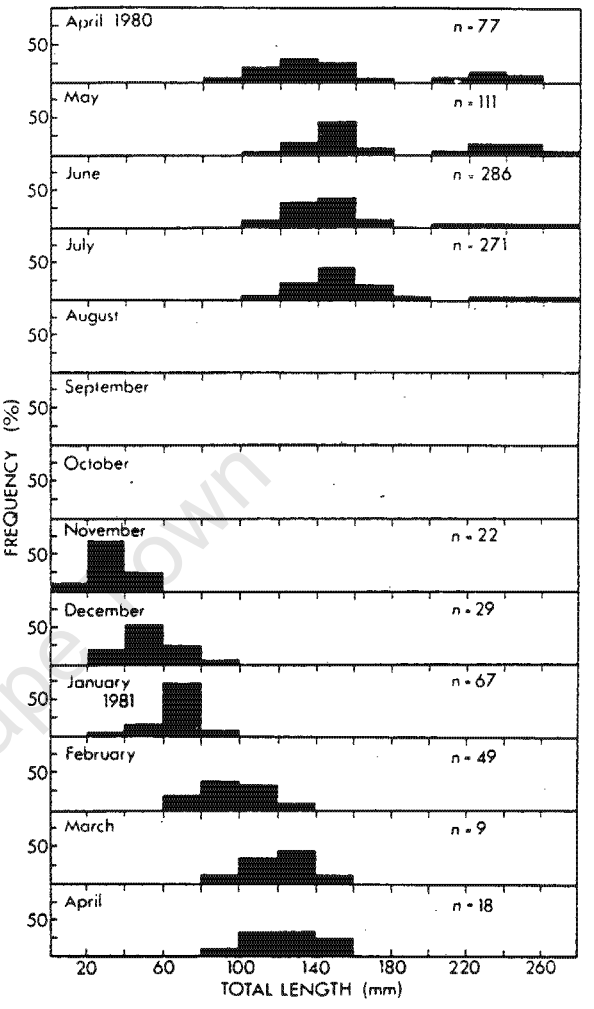

Fig. 6: Monthly size distribution of *Lithognathus lithognathus* in the Kleinmond Estuary

pattern was the presence of *L. richardsoni* of the 0+ group in the Bot Estuary between January and March. This was, as already stated, due to their intrusion from the Kleinmond Estuary between late December and January when water was passing through the channel spillway between the two. It can therefore be assumed that, as with the other twelve species, these *L. richardsoni* had also originated from the sea. The view that the 13 species were the product of a recent spawning at sea is consistent with their small size at the time of recruitment into the Palmiet and Kleinmond estuaries and with the fact that these species do spawn at sea (Wallace 1975, Day *et al.* 1981). Moreover, the size at which they were caught corresponds to that which would normally be obtained during the first six months of life.

Gill-netting showed that individuals of all 13 marine species were often abundant in the deeper offshore waters of the Bot Estuary at a size in excess of that at which they attain maturity (Bennett *et al.* 1985). Although some specimens did contain active gonads as defined in Table I, ripe gonads were never observed (Bennett *et al.* op. cit., this study). Therefore, it is likely that these species do not actually spawn in estuaries of the South-Western Cape, at least in those three studied.

Of the 13 marine species listed in Table V, 10 spawn during winter and spring. Information collected during the current study demonstrates that juveniles are recruited into the Kleinmond and Palmiet estuaries during spring and summer, approxi-

Table V: Lengths at recruitment, lengths at maturity, lengths at one year old, spawning seasons and months in which marine migrant species recruited into the Palmiet and Kleinmond estuaries

Species	Length at recruitment	Approx. length (mm)		Spawning season	Months of recruitment												
		1 year old	Maturity		A 1980	M	J	J	A	S	O	N	D	J 1981	F	M	A
Diplodus sargus	40-60	-	150[7]	Summer[14]		*										*	
Lichia amia	50-120	220[1]	550[7]	Spring[7]									*	*	*	*	
Lithognathus lithognathus	18-50	160	500[8]	Winter[8]							*	*	*	*	*		
Liza dumerili	40-60	-	240[7]	Winter/spring[7]	*	*											*
L. richardsoni	17-50	75[2]	250[7]	Summer[15]	*	*	*	*	*	*	*	*	*	*	*	*	*
L. tricuspidens	120	-	440[7]	Winter/spring[12]		*											
Mugil cephalus	20-50	200[3]	340[10]	Winter[7]						*	*					*	
Mexus capensis	20-40	115[3]	280[11]	Winter[11]	*	*				*	*	*	*	*		*	*
Pomatomus saltatrix	40-120	160[4]	280[12]	Spring[12]									*	*		*	
Rhabdosargus globiceps	20-40	80[5]	260[5]	Summer[7]										*	*	*	*
R. holubi	15-40	60[1]	180[7]	Winter[7]	*						*			*	*	*	*
Sarpa salpa	40-60	90[6]	170[13]	Winter[9]												*	
Solea bleekeri	40-55	-	100[9]	Winter[9]								*		*		*	
Number of species recruiting					4	5	1	1	1	3	5	4	5	8	5	10	5

References:
1. Blaber (1974), 2. Ratte (1977), 3. Bok (1984), 4. Van der Elst (1976), 5. Talbot (1955), 6. Lasiak (1983a), 7. Day *et al.* (1981), 8. Mehl (1973), 9. Wallace (1975), 10. Whitfield and Blaber (1978), 11. Bok (1983), 12. Van der Elst (1981), 13. Joubert (1981), 14. Coetzee (1986), 15. Lasiak (1983b)

mately 2–4 months after spawning and at lengths usually less than 25 mm (Table V). The fish then remain in the estuaries until winter before returning to sea. An example of the manner in which these marine migrant species use estuaries is provided by the data for *Lithognathus lithognathus* in the Kleinmond Estuary (Fig. 6). Recruitment in 1980 took place in November and December, at which time fish length ranged from 18 to 50 mm. By April 1981, when sampling ceased, these recruits had grown to a mean length of 125 mm. Two size groups were present when sampling was initiated in April 1980, the modal length classes of which were 120–139 mm and 220–239 mm (Fig. 6). The similarity of the length distributions of the first group with those of the sample of 0+ fish taken in April the previous year is a strong indication that they represent fish which are approximately nine months of age. The discreteness and the limited range in length of the second group in April 1980 suggest they represent fish that are one year older. The two groups can each be clearly followed through the length-frequency histograms between April and July 1980. The total absence of this species between August and October presumably reflects their having vacated the estuary during the periods of heavy freshwater discharge in the winter.

Migrants were the most important component of the fish community in the permanently open Palmiet Estuary, where they constituted 73 per cent of the species and 53 per cent of the numbers of fish caught (Table VI). The same group was less important in the seasonally open Kleinmond Estuary (61% spp., 19% numbers) and, although they provided 36 per cent of the species taken from the Bot Estuary, they contributed only 1 per cent of the total numbers caught.

Utilization of estuaries by resident species

Unlike the marine migrant species listed in Table V, the seven teleosts named in Table VII were caught in the Bot Estuary at sizes corresponding to those which would be expected, from knowledge of their approximate growth rate, during their first year of life. As the Bot Estuary had been closed for the previous 32 months, it is assumed, therefore, that all seven of these species spawned within the estuary during that period. Such a conclusion is supported by the observation that ripe-running and recently spent females of each species were also caught in the estuary. Therefore, it is concluded that these species form the resident component. They are overwhelmingly dominant in the Bot Estuary, providing 99 per cent of the total number of fish caught and half the species (Table VI). They were of lesser importance in

Table VI: Percentage composition (species and numbers) of migrant and resident species in the Palmiet, Kleinmond and Bot estuaries

Estuary	% species			% numbers		
	Migrants	Residents	Freshwater	Migrants	Residents	Freshwater
Palmiet	73	27	0	53	47	0
Kleinmond	61	33	6	19	81	1
Bot	36	50	14	1	99	0

the Kleinmond (33% spp., 81% numbers) and Palmiet estuaries (27% spp., 47% numbers).

Examples of the means whereby the size structure of populations of resident species changes seasonally in the Bot Estuary are provided by *Atherina breviceps* and *Clinus spatulatus* (Figs 7 and 8). Data from *Gilchristella aestuaria* were too sparse to allow such analysis. Spawning of *A. breviceps* takes place between late spring and late summer (Table VII). The 0+ age class in April 1980 is represented by a sharply defined modal length class of 20–30 mm (Fig. 7). This mode can be traced clearly through the samples obtained in subsequent months until November, by which time it had reached 50–59 mm (Fig. 7). The presence of an identical mode in January, March and April shows that little growth occurs when this species reaches sexual maturity at the end, apparently, of its first year of life. While some *A. breviceps* longer than 70 mm were caught in April and May 1980, no fish of the same size were taken during the following three months. This implies that, within the Bot Estuary, *A. breviceps* generally dies after the first spawning season.

The only representative of *C. spatulatus* found outside the Bot Estuary was a large specimen caught in the Kleinmond Estuary (Bennett 1983). The species bred primarily between May and August in 1980 (Table VII). While a modal length class was not always well defined in the samples of *C. spatulatus* taken between July 1980 and April 1981 (Fig. 8), it would appear reasonable to assume that the mode of 70–79 mm in March and April 1981 corresponds to the 0+ age class, which in the previous July had ranged from 20–49 mm with a mode at 20–39 mm (Fig. 8). Such a view is consistent with the fact that the mode in March and April 1981 compares with a similar single one caught in April 1980. The trends in growth of the latter group during subsequent months in 1980 and 1981 (determined solely on the basis of modal progression) shows that this group does not start increasing markedly in length until the onset of spring.

DISCUSSION

Classification and ordination revealed marked seasonal changes in the structure of the fish communities of the Palmiet and Kleinmond estuaries. Thus, in the Palmiet, the samples from winter (June–August) clustered separately from those in autumn (March and April) and spring/summer (October–February). The results for May are complicated by the fact that they were dominated by an exceptionally large catch of 3 900 *Atherina breviceps*, some 98 per cent of the total catch of this species. The separation of the winter from the autumn samples reflects the eflux of

Table VII: Lengths at 50-per-cent maturity, minimum lengths and the months in which ripe individuals of seven fish species which reproduce in estuaries of the South-Western Cape were sampled

Species	Minimum length caught (mm)	Length at maturity (mm)	Breeding season											
			A	M	J	J	A	S	O	N	D	J	F	M	A
Atherina breviceps	16	43						★	★	★	★	★	★	★	
Caffrogobius multifasciatus	23	60	★					★		★	★	★		★	
Clinus spatulatus	20	75		★	★	★	★								
Gilchristella aestuaria	17	34						★	★	★		★	★	★	★
Hyporhamphus capensis	42	100							★		★				
Psammogobius knysnaensis	19	37						★	★	★	★	★	★		
Syngnathus acus	41	125							★		★	★		★	★
Number of species breeding			1	1	1	1	1	4	5	4	5	5	3	4	2

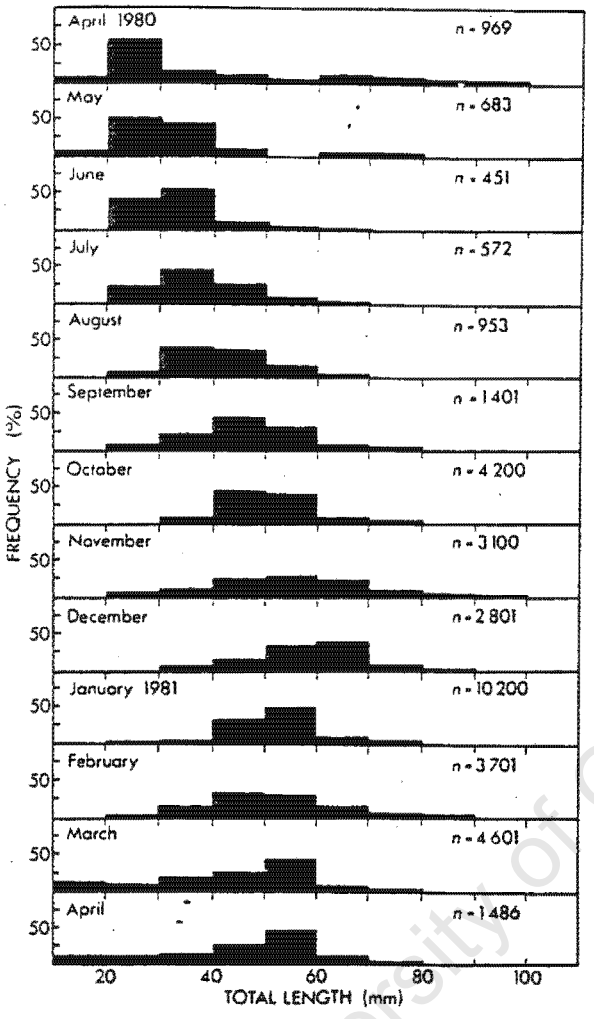

Fig. 7: Monthly size distribution of *Atherina breviceps* in the Bot Estuary

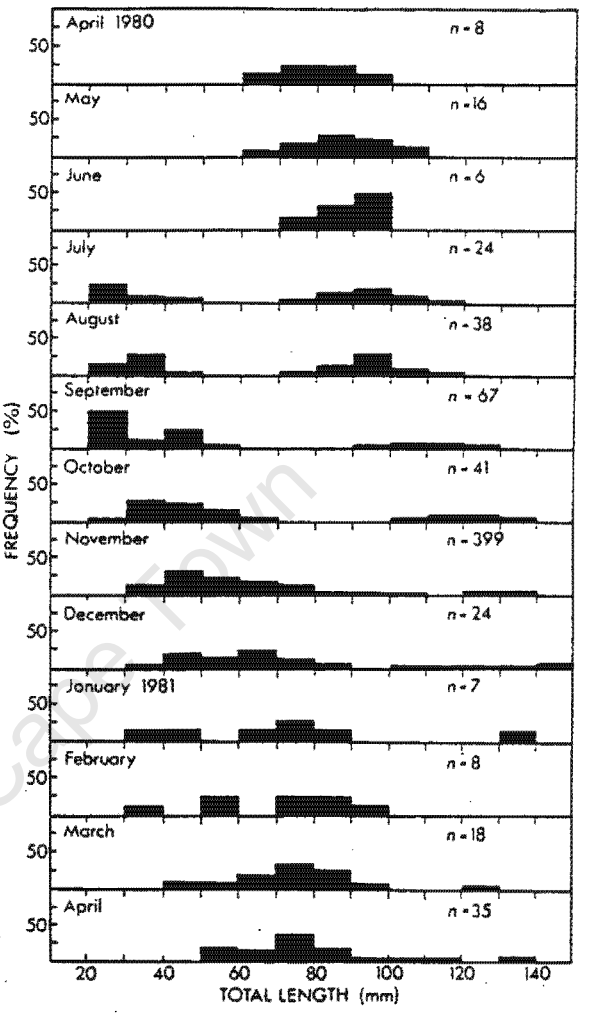

Fig. 8: Monthly size distribution of *Clinus spatulatus* in the Bot Estuary

marine migrants during heavy freshwater discharge. The separation of the spring/summer samples from those of winter in turn reflects the immigration of new 0+ recruits of marine species. While the picture is essentially the same in the Kleinmond Estuary, the "winter" samples do not group separately until August–October. This is clearly attributable to the fact that the bar is not breached until July and therefore migrants cannot leave the estuary as early as they do in the Palmiet. There were no marked seasonal changes in the community structure of the Bot Estuary, a feature that can be related to its having remained closed. In this context, it is significant that the number of species did not decline as much in winter as it did in the other two systems.

It seems clear, therefore, that the marked seasonal patterns exhibited by the fish communities of the two estuaries which were open for some time during the study period should be relatable to seasonal climatic changes. The marine migrant species which utilize these estuaries breed primarily during winter, resulting in their larvae and small juveniles being present inshore in spring and early summer. At this time of year the winter floods have abated and water temperatures are increasing, but the seasonally and intermittently open estuaries have yet to close. Small

juveniles can therefore enter the estuaries and remain there until the onset of the next winter.

Resident species have reproductive specializations which enhance the chances of their eggs being retained within estuaries. *Clinus spatulatus* is ovoviviparous, releasing live young 20 mm long. Male *Syngnathus acus* retain eggs and larvae in a brood pouch. *Atherina breviceps*, *Caffrogobius multifasciatus*, *Hyporhamphus capensis* and *Psammogobius knysnaensis* all lay large eggs with threads which attach to some fixed substratum. Only *Gilchristella aestuarius* has free-floating eggs (Wooldridge and Bailey 1982), though Talbot (1982) states that, in the Swartkops Estuary (33°52'S, 25°38'E) at least, these are spawned in the extreme upper reaches. Loss of eggs to the sea by these species is further reduced by the fact that all except *C. spatulatus* breed during summer, when rainfall is at a minimum and most of the estuaries are closed or, if open, water currents are at a minimum. Further advantages of summer spawning are that aquatic macrophytes and invertebrate populations will have recovered from stranding and scouring of the previous winter by the time hatching occurs. Maximum cover and food are available and high temperatures prevail, conditions that will optimize growth of larvae and juveniles. By the following winter, therefore, most juveniles will have attained sufficient size to have some chance of withstanding the adverse conditions.

The data presented in this paper have shown that differences in the number, composition and abundance of species in the three studied estuaries of the South-Western Cape can be related to whether or not each estuary had been closed and if so for how long. Thus, the permanently open Palmiet Estuary has the highest percentage of migrant species and the closed Bot Estuary the lowest, with resident species following the opposite trend. When numbers of fish are considered, these trends become even more marked. Migrants contributed only 1 per cent and residents 99 per cent to the catch in the Bot Estuary, whereas the two groups occurred in approximately equal abundance in the Palmiet. In estuaries closed throughout the year, such as the Bot, migrant species are unable to leave or enter, and the only changes that take place are due to mortality (Blaber 1973, Bennett *et al.* 1985) or changes in the abundance cycles of species able to breed in the estuary. There are marked seasonal changes in the estuaries open for all or part of the year. During winter, when freshwater input and outflowing currents are strong and temperatures and salinity are low, few individuals and species are present. As the dry season commences, freshwater discharge declines, temperatures rise and species enter the estuaries in increasing numbers. These fish may be trapped until the estuary opens the following winter or they may leave if the estuary is open at the onset of cooler conditions.

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CHAPTER 7.

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SPECIAL PUBLICATION

No. 29

CLINUS SPATULATUS, A NEW SPECIES OF CLINID FISH (PERCIFORMES: BLENNOIDEI) FROM SOUTH AFRICA, WITH A MODIFIED DEFINITION OF THE GENUS *CLINUS*.

by

B.A. Bennett

GRAHAMSTOWN, SOUTH AFRICA

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ABSTRACT

Bennett, B.A. 1983. *Clinus spatulatus,* a new species of clinid fish (Perciformes: Blennoidei) from South Africa, with a modified definition of the genus *Clinus*. *J.L.B. Smith Institute of Ichthyology, Special Publication* No. 29, 9 pages, 6 figures.

Clinus spatulatus sp. n. is described from 50 specimens collected from an estuary in the southwestern Cape Province, South Africa. The presence of supraorbital tentacles or papillae distinguishes *Clinus* and *Gynutoclinus* from other South African genera of the subtribe Clinidi. The new species has simple supraorbital tentacles, an intermediate condition between the well-developed, at least bifid tentacles of *Clinus* and the simple supraorbital papillae of *Gynutoclinus*. For this reason Penrith's (1969) diagnosis of *Clinus* is modified to include the new species as well as the monospecific *Gynutoclinus* thereby incorporating all South African species with supraorbital papillae or tentacles.

The publication of this paper has been assisted by a grant from the South African Department of National Education.

CLINUS SPATULATUS, A NEW SPECIES OF CLINID FISH (PERCIFORMES: BLENNOIDEI) FROM SOUTH AFRICA, WITH A MODIFIED DEFINITION OF THE GENUS *CLINUS*.

by

B.A. Bennett[1]

During an ecological study of fish inhabiting southwestern Cape estuaries an unusual species of clinid was discovered. This species, although clearly referable to the subtribe Clinidi Hubbs and superficially similar to many southern African clinids, was found to differ from all previously described South African species, especially with regard to the shape of its supraorbital tentacles.

Supraorbital tentacles are regarded as important morphological features in determining generic placement within the South African Clinidi. Smith (1945) divided the South African Clinidae into two subfamilies, the Clininae, containing those species possessing a "fringed" supraorbital tentacle and the Myxodinae, with no tentacle over the eye. He placed *Clinus rotundifrons* (Barnard) into the new genus *Gynutoclinus* in the non-tentacled group, but as Penrith (1965) pointed out, they do in fact have a small papilla over the eye. In the most recent revision Penrith (1969) established five genera of which *Clinus* had "at least bifid" tentacles; *Gynutoclinus* a "minute simple papilla" over the eye while the other three genera lacked tentacles.

The species to be described below is intermediate between *Clinus* and *Gynutoclinus* in the shape of its supraorbital tentacles. At one extreme the supraorbital tentacles are minute and papillose (Fig. 1A), resembling those of *Gynutoclinus,* and on the other they are elongated and bifid (Fig. 1E), a condition sometimes present in some *Clinus* species. Most of the specimens, however, had well-developed simple tentacles (Fig. 1B & C), intermediate between those of *Gynutoclinus* and *Clinus,* it is therefore suggested that all South African clinids possessing supraorbital projections be included in the diverse genus *Clinus.*

Australian and Indo-Pacific clinids are in need of revision. Of the six genera in current use only *Cristiceps* has been generally regarded as distinct. The status of *Clinus, Heteroclinus, Neoblennius, Petraites* and *Springeratus* is discussed by Penrith (1969), McKay (1970), Shen (1971), Fraser (1972) and Hoese (1976) and will not be considered further in this paper. Supraorbital tentacle characteristics are not important in placing species among the above genera, thus the proposed modification of the South African genus *Clinus* will not affect the taxonomy of the group as a whole.

The subdivision of *Clinus* into subgenera is discussed by Penrith (1969; 16-19). She used five subgenera, one containing a large number of generalised species and the other four representing particular lines of development. *Clinus rotundifrons,* the type-species of the genus *Gynutoclinus,* differs from other species of the subgenus by having a more compressed body and a more rounded head. These differences represent only an extension in the range of body form shown by this group and are therefore not considered sufficient to set *Gynutoclinus* apart as a separate subgenus.

Measurements and terminology used in the description follow Penrith (1969).

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Genus *Clinus* Cuvier, 1816

Clinus Cuvier, 1816: 251 (type-species *Blennius acuminatus* Bloch & Schneider, 1801 by subsequent designation by Swainson, 1839: 75).

Cirrhibarbis Valenciennes, in Cuv. & Val., 1836: 406 (type-species *Cirrhibarbis capensis* Valenciennes, in Cuv. & Val., 1836 by monotypy).

Blennophis Swainson, 1839: 75 (type-species *Clinus anguillaris* Valenciennes, in Cuv. & Val., 1836 by monotypy).

Ophthalmolophus Gill, 1860: 104 (type-species *Clinus latipennis* Valenciennes, in Cuv. & Val., 1836 by monotypy).

Climacoporus Barnard, 1935: 646 (type-species *Climacoporus navalis* Barnard, 1935 by monotypy).

Nemacoclinus Smith, 1937: 195 (error for *Climacoporus Barnard).*

Muraenoclinus Smith, 1945: 538 (type-species *Clinus dorsalis* Castelnau, 1860 by monotypy).

Blenniomimus Smith, 1945: 538 (type-species *Clinus taurus* Gilchrist & Thompson, 1908 by original designation).

Caboclinus Smith, 1966: 73 (type-species *Clinus robustus* Gilchrist & Thompson, 1908 by original designation).

Gynutoclinus Smith, 1945: 545 (type-species *Clinus rotundifrons* Barnard, 1937 by monotypy).

NOTE: According to C. Roux (1976, *J. Soc. Bib. Hist.* 8(1): 31), volume 2 of the first edition of Cuvier's *Le Règne Animal* was published in 1816, not 1817 as is usually cited. The genus *Cirrhibarbis* was attributed to Cuvier, 1817 by Penrith (1969: 14,25), but this genus was not mentioned in the first edition of *Le Règne Animal.* It was indicated, but only in the vernacular form "Les Cirrhibarbes", in the second (1829) edition. The genus *Cirrhibarbis* must then be attributed to Valenciennes, *in* Cuv. & Val., 1836.

DIAGNOSIS: (Modified from Penrith 1969: 14). A papillose, simple or fringed tentacle over eye. Lateral line usually of double pores and/or single pores opening above and below line anteriorly; posterior to post-pectoral curve usually of short separate horizontal tubes with a pore at either end. Intromittent organ of male usually consists of fairly long basal portion with small tip retractile between one or two pairs of fleshy lips. Body covered with small embedded cycloid scales. Two bands of villiform teeth in each jaw, outer row larger. Vomer toothed. Upper jaw averages more than 40% head length. Vertebrae (15-21) + (27-40).

Subgenus *Clinus* Cuvier, 1816

Synonyms: *Ophthalmolophus* Gill, 1860; *Blenniomimus* Smith, 1945; *Gynutoclinus* Smith, 1945.

DIAGNOSIS: Body not elongate. Head naked; no barbels on chin or snout. More than one dorsal soft-ray. Vertebrae (15-18) + (27-33).

Clinus (Clinus) spatulatus sp. n.

(Figs. 1 + 2)

HOLOTYPE: South African Museum (SAM) No. 29449: female, 78.5 mm SL; Botriviervlei, southwestern Cape Province, South Africa (34°21'S 18°07'E); 6 April 1981; B.A. Bennett, collector.

PARATYPES: (All paratypes were collected at the same locality as the holotype from May 1980 to April 1981.) SAM 29450: male, 86.6 mm SL; SAM 29451: 10,22.5-133.6 mm SL. Australian Museum (Sydney) No. I.23903-001: 6,67-88 mm SL. Bernice P. Bishop Museum (Honolulu) No. 28955: 6,29-84 mm SL. National Museum of Victoria (Melbourne) No. A3177: 5,61-66 mm SL. JLB Smith Institute of Ichthyology (Grahamstown) No. 18239: 13,28-114 mm SL. United States National Museum (Washington, D.C.) No. 259352: 5,43-72 mm SL.

DIAGNOSIS: pectoral rays 13-15; dorsal soft-rays 6-8; pelvic rays 3; gill-rakers (2-4) + (6-8); and vertebrae (17-18) + (28-29). This species may be distinguished from all other members of the subgenus in usually having elongate, simple supraorbital tentacles.

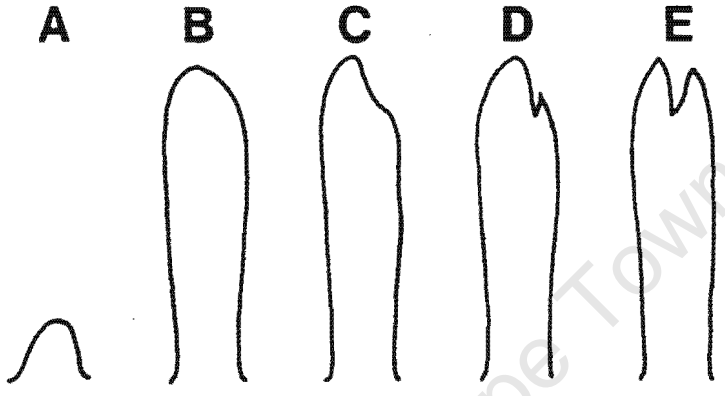

Figure 1. Range of supraorbital tentacle shapes observed in a sample of 50 *Clinus spatulatus*. Number of fish with tentacles of a particular shape or, where bilaterally asymmetrical, combination of shapes as follows: A = 0, AB = 2, B = 30, BC = 5, C = 6, CD = 3, D = 2, DE = 2, E = 0.

DESCRIPTION: Based on 50 specimens 20-150 mm SL (Fig.4). See Table 1 and Figure 3 for frequency distributions. D XXXII-XXXV,6-8; A II,23-25; P 13-15; V I,2-3; C 13. Vertebrae (17-18) + (28-29). Gill-rakers in outer series on first arch (2-4) + (6-8). Dorsal fin with first 3 spines elevated to form a crest, considerably higher in mature males than in females (Fig. 3A). Notch in membrane between third and fourth dorsal spines (45-100% of fourth spine free, Fig. 3B). No clusters of cirri at tips of dorsal spines. Pectoral fin rounded. Inner pelvic ray reduced and not free from membrane.

Caudal peduncle length and depth 27-38% head length. Caudal fin subtruncate. Body slightly compressed, not elongate, covered with small embedded scales more or less overlapping on front half of body, not extending onto fin bases; head naked. Depth 3.8-5.0 in SL (juveniles < 40 mm SL more elongate Fig. 3C); head 3.5-4.4 in SL, becoming proportionately more robust with increasing length, especially in males. Eye 2.5-3.7 in head (2.5-2.8 in juveniles); Upper jaw 1.8-3.0 in head. Interorbital convex. Supraorbital tentacle small (Fig. 3D), subcylindrical basally usually with a simple spatulate tip (Fig.1). Cirrus on anterior nostril flap-like on a tubular pedicel. Sensory pores of head variable; often double in supraorbital, postorbital, occipital and upper preopercular series, single elsewhere (Fig. 2B).

Lateral line (Fig. 2C), from its origin to upper portion of post-pectoral curve of single pores opening above and below the line and some vertical pairs of pores, thereafter of separate horizontal tubes with pores at each end, becoming indistinct posteriorly. Intromittent organ of male (Fig. 2D) moderately long with thick basal portion, tip almost entirely ensheathed by confluent ventral lips with two smaller indistinct dorsal lips set further back.

Coloration: Variable and sexually dichromatic in adults. Females and small juveniles usually with olive ground colouration underlying a darker irregular blotched and mottled pattern in varying shades of green and/or brown. Ground colour usually dominates in the region of the median fin bases and along posterior lateral line area. Mature males usually uniformly dark grey or brown, appearing almost black; often with small, pale patches on opercula, pectoral-fin bases and around posterior portion of lateral line. Pattern remains for at least two years after preservation in formalin.

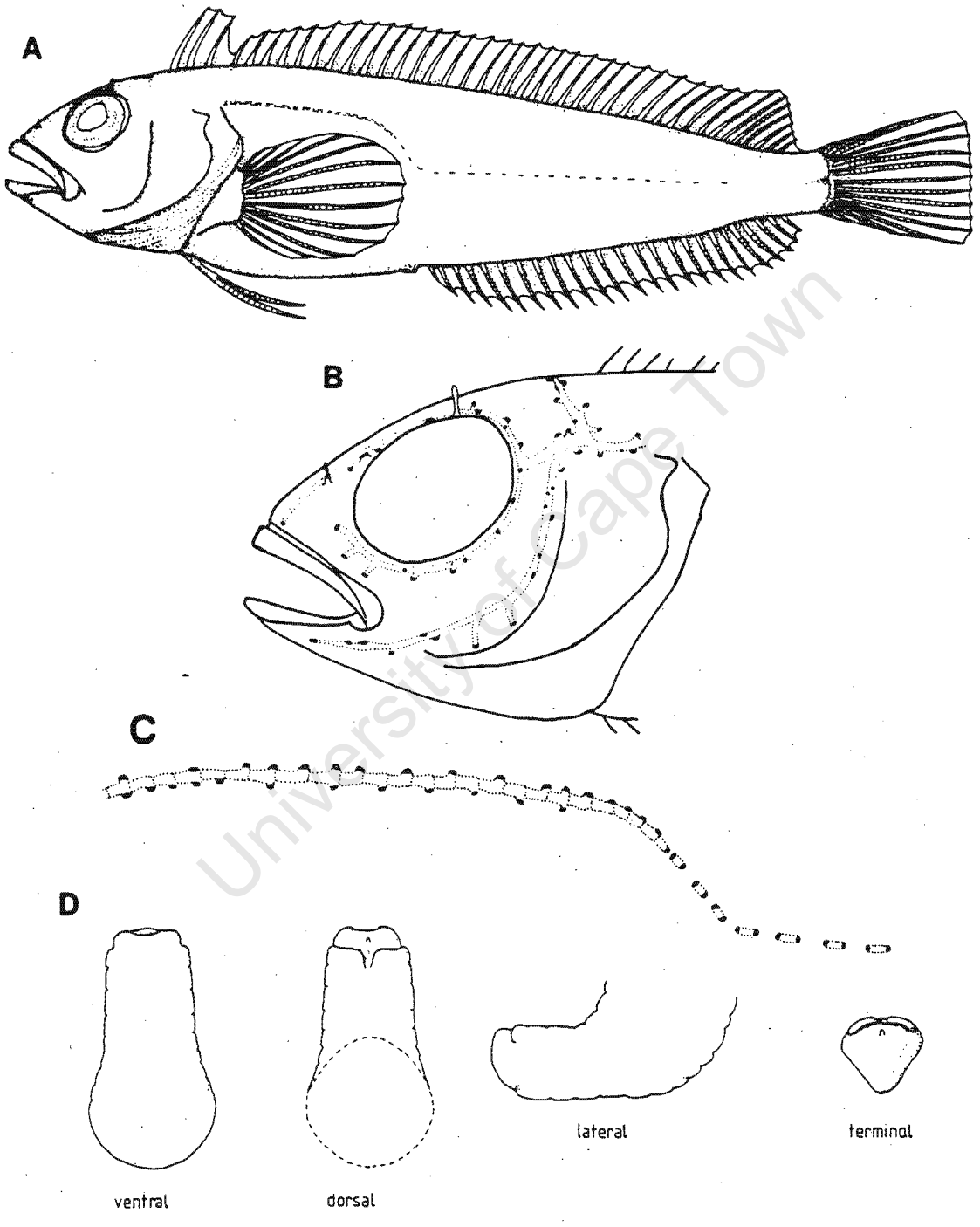

Figure 2. *Clinus spatulatus:* A) Lateral view of female 85 mm SL, SAM 29449. B) Head pore system. C) Lateral line. D) Intromittent organ of male.

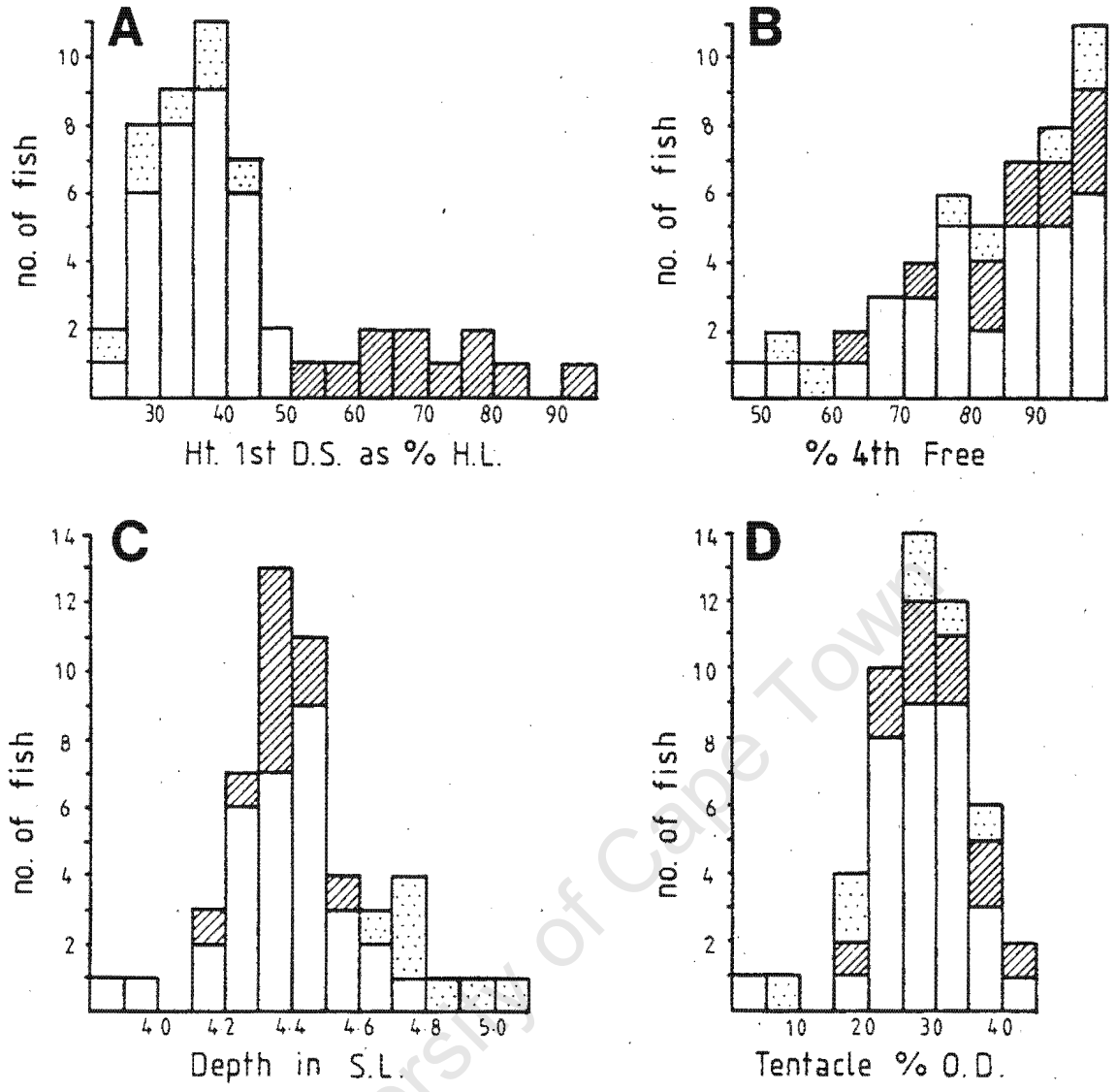

Figure 3. Variation in morphological features observed in a sample of 50 *Clinus spatulatus:* A) Height of fourth dorsal spine as percentage of head length. B) Percentage of fourth dorsal spine free from membrane along its anterior edge. C) Standard length/body depth at anal fin origin. D) Height of left supraorbital tentacle as percentage of maximum orbit diameter. (Clear area = females, hatched = males, stippled = juveniles.)

COMPARISONS: *Clinus spatulatus* is similar to *C. superciliosus, C. woodi, C. robustus, C. brevicristatus, C. taurus* and *C. agilis* in having a notch in the membrane between the third and fourth dorsal spines but can be separated from these species as follows: it has 13-15 pectoral rays (15-18 in *C. superciliosus,* 12 in *C. robustus* and *C. taurus*); it has 7 or 8 dorsal soft-rays, more than *C. taurus, C. woodi* and *C. agilis* but less than *C. robustus;* it has 28 or 29 caudal vertebrae whereas *C. superciliosus* has 30-32; *C. woodi* and *C. taurus* have 15 or 16 precaudal vertebrae, the new species has 17 or 18; *C. brevicristatus* has 3 pelvic rays free from the membrane and 2-4 ceratobranchial gill-rakers, the new species has 2 free pelvic rays and 6-8 ceratobranchial gill-rakers.

DISTRIBUTION: To date known only from the Botriviervlei and Kleinmond estuary (34°21'S, 18°07'E) in the south-western Cape Province, South Africa.

REMARKS: A single specimen (SAM 21938, female; see Penrith 1965b for description), with supraorbital tentacles very similar to those of *Clinus spatulatus* was collected from Richards Bay, Kwazulu (date and collector unknown). The specimen differs from *C. spatulatus* in having a considerably more rounded head profile and scales extending onto the caudal fin base; these features may be sufficient to justify its description as a separate species but this is considered inadvisable because only one individual is available for study.

ETYMOLOGY: *spatulatus* (Latin, adjective) — a reference to the shape of the supraorbital tentacle.

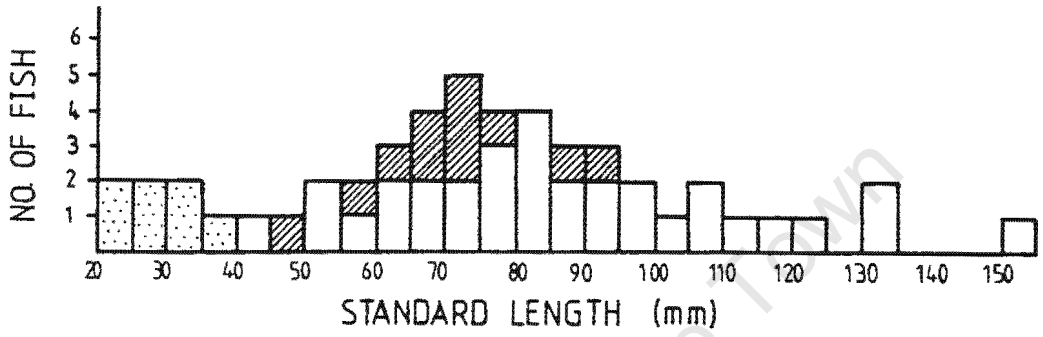

Figure 4. Size distribution of 50 *Clinus spatulatus* on which the description is based. Clear area = females, hatched = males, stippled = juveniles.

ECOLOGY: Monthly samples of fish were collected from three different localities in the Botriviervlei between May 1980 and April 1981. The estuary was isolated by a sand bar during the period sampled, having last been in contact with the sea at the end of 1977. Temperatures varied between 13.9°C and 24.5°C and salinities between 7‰ and 15‰ (Coetzee 1982). Salinities subsequently fell to 2‰ in October 1981 resulting in mass fish mortality. However, no *C. spatulatus* were observed to have died as a result of the low salinities.

Clinus spatulatus is the only South African clinid having its major population in an estuary. All seine hauls were made in marginal areas at depths of less than 1.7 m . These areas were vegetated by dense stands of aquatic macrophytes, predominantly *Ruppia maritima* and *Cladophora* sp. but also including *Potomageton pectinatus* and *Chara* sp. Rocky areas were not sampled and it is therefore not known whether *C. spatulatus* occur in these areas.

C. spatulatus occurred in 80.6% of the 36 seine hauls and was numerically the fourth most abundant species in the catches, occurring in an estimated density of 0.04 fish m^{-2} (0.08 g m^{-2}). The three most abundant species were *Hepsetia breviceps, Gilchristella aestaurius* and *Psammogobius knysnaensis.*

The contents of 50 stomachs (Fig. 6) were analysed using the occurrence and volume methods (see Hynes 1950). Amphipods, mainly *Melita zeylanica* and *Corophium trienonyx,* occurred in 93.6% of stomachs and comprised 31.6% of the total volume of food consumed. Isopods, represented almost entirely by *Exosphaeroma hylecoetes,* occurred in 63.8% of guts and provided 34.9% of the volume. Other important dietary constituents were gastropods (*Tomichia* sp. and *Hydrobia* sp.) at 12.8% occurrence and 22.6% by volume respectively and insects, mainly chironomid larvae, which occurred in 52.5% of guts and constituted 3.7% of the volume. *Clinus spatulatus* is therefore a generalist carnivore, consuming very similar prey to marine clinids in the same area (see Bennett et al. 1983 in press).

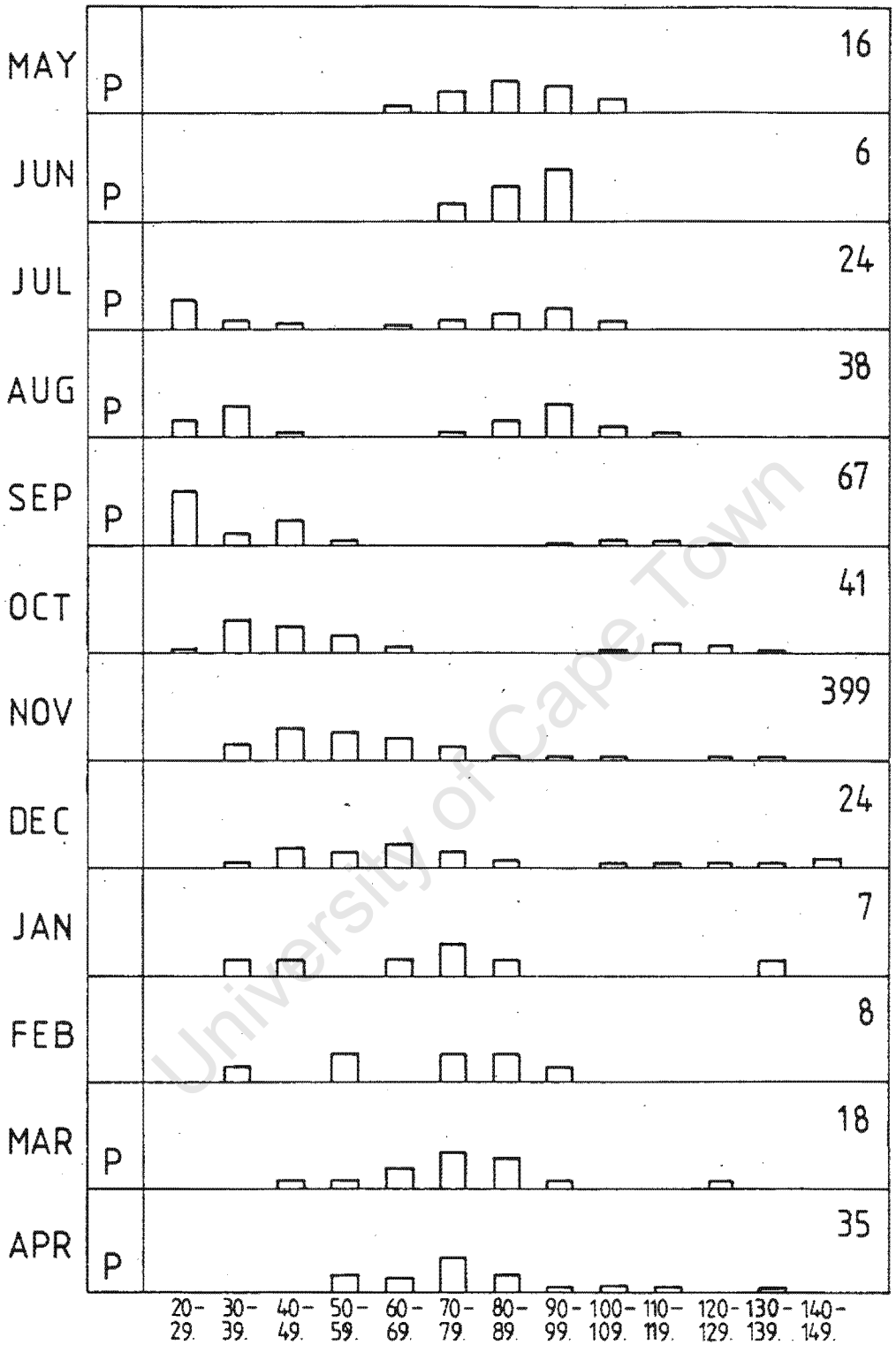

Figure 5. Size/frequency distribution of *Clinus spatulatus* sampled at monthly intervals from Botriviervlei. Shifts in modal sizes give an indication of growth. Months in which at least one female contained embryos exceeding 15 mm TL are marked "P" in the left column.

REPRODUCTION: The sex ratio of *C. spatulatus* in the catch was one male to approximately 15 females. Females appear to mature in their first year at a length of 75-80 mm TL. Embryos in an advanced stage of development (>15 mm) were present between March and September and small juveniles (20-40 mm) appeared in the catches between July and September.

GROWTH: Apparent growth, estimated from modal progressions (Fig.5), was 5.4 mm TL mth^{-1}. Modal size increased from 25 to 90 mm TL in one year. Few fish appeared to survive for more than 18 months by which time they had attained a size of approximately 130 mm TL. The largest specimen, a female taken from the adjacent Kleinmond estuary, was 172 mm TL.

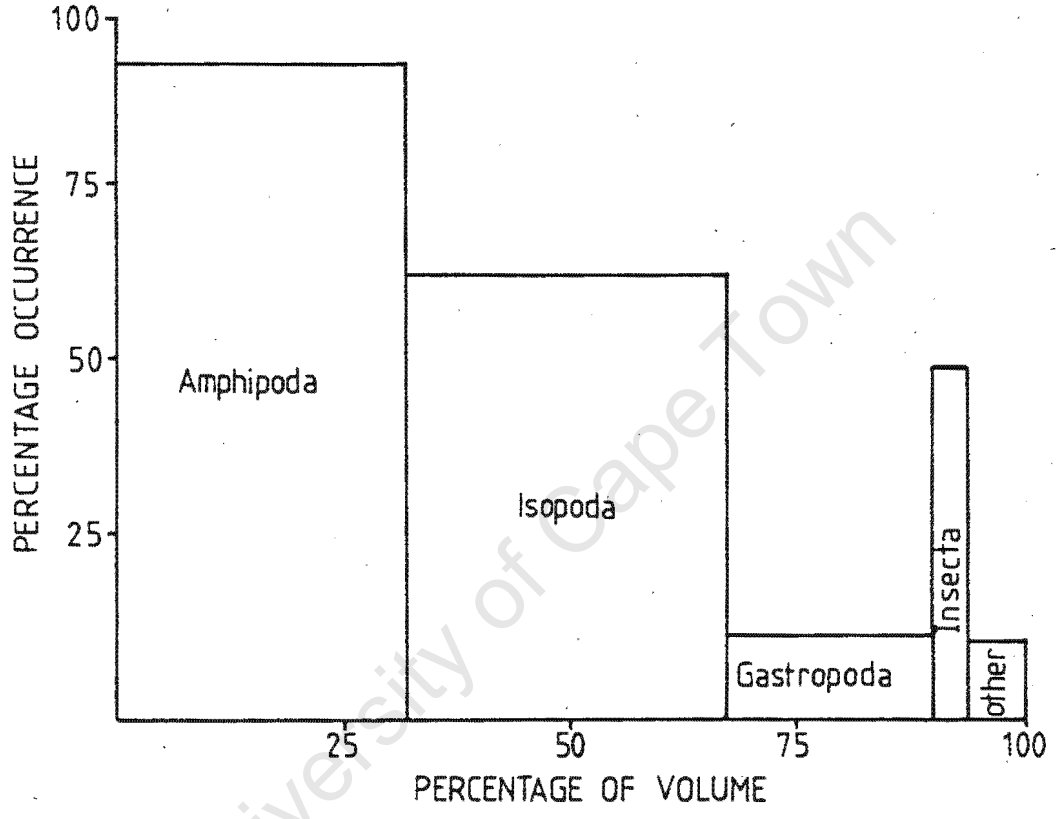

Figure 6. Relative importance of major food items consumed by *Clinus spatulatus*.

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I would like to thank Dr C.L. Griffiths (Zoology Department, University of Cape Town) and Miss E. Louw (S.A.M.) for their helpful guidance and for reviewing drafts of the manuscript, Professor G.M. Branch (Zoology Department, UCT) for his enthusiastic supervision of the estuarine fish project, and Professor M.M. Smith (RUSI) for confirming that the new species was undescribed and encouraging me to write this paper.

I am grateful to the South African Nature Foundation (affiliated to the World Wildlife Fund) who funded the work during which the specimens and ecological data were collected and to the South African National Council for Oceanographic Research for financial support through their Benguela Ecology Programme, my employer during the time that this manuscript was prepared.

TABLE 1. Variation in meristic characters of a sample of *Clinus spatulatus*.

Number of elements	2	3	4	5	6	7	8	...	13	14	15
Dorsal fin rays					1	31	18				
Pelvic fin rays	2	18									
Pectoral fin rays									12	37	1
Epibranchial gill-rakers	3	15	2								
Ceratobranchial gill-rakers					2	16	2				

Number of elements	17	18	....	23	24	25	....	28	29	....	32	33	34	35
Precaudal vertebrae	1	19												
Caudal vertebrae								1	19					
Anal fin rays				10	16	24								
Dorsal fin spines											1	15	24	10

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CHAPTER 8.

Suid-Afrikaanse Tydskrif vir Wetenskap Vol. 80 Mei 1984

South African Estuaries and Their Importance to Fishes

J. H. Wallace, H. M. Kok, L. E. Beckley, B. Bennett, S. J. M. Blaber and A. K. Whitfield

In this article environmental conditions typical of South African estuaries are contrasted with those of marine inshore waters in order to emphasize that estuarine fishes comprise a specialised component of the marine fauna. The life cycle of estuarine fishes is described and related to important physical and biological characteristics of estuaries. The fish fauna is divided into six categories according to the extent of their dependence on estuaries. This is followed by discussion of the effects of estuarine degradation on these groups. It is concluded that continuing degradation will result in a decline in South Africa's estuarine fish fauna and consequently in recreational angling, in the yield of high-protein food and in economic activities dependent upon this natural resource. It is recommended that higher priority be accorded to the conservation of estuaries in the face of development projects that impinge on this environment.

South Africa's estuaries represent an extremely valuable national resource which is increasingly threatened by urban, industrial and agricultural development. Whereas development goals and conservation ideals can sometimes be reconciled, this is the exception rather than the rule and in the past development has all too often been unsympathetic to the environment and resulted in permanent damage to South African estuaries. Perhaps one of the reasons for this is that the case for conservation has not been sufficiently clearly stated.

There are many reasons for conserving estuaries, not the least of which is their recreational value and it is in this respect that fish and fishing are particularly significant. The authors of this article are specialists in the study of estuarine fish and are consequently able to present an authoritative statement on South African estuaries, their importance to fishes and the need for greater attention to be given to their conservation.

J. H. Wallace and H. M. Kok are on the staff of the Port Elizabeth Museum, P.O. Box 13147, Humewood 6013, South Africa; L. E. Beckley and B. Bennett are in the Zoology Department, University of Cape Town; S. J. M. Blaber is in the Department of Zoology, University of Natal, Pietermaritzburg; and A. K. Whitfield is in the Institute for Freshwater Studies, Rhodes University.

Basic facts about the estuarine environment and estuarine fishes

Conditions in South African estuaries differ markedly from those that prevail in the sea. The marine inshore waters adjoining the Republic's 3000-km coastline is typified by turbulent wave action, a lack of sheltered shores, and by a narrow continental shelf on the east and south-east coasts. In contrast, the estuarine environment is very much smaller in area, is typically calm, sheltered and shallow, as well as being subject to greater variation in salinity, turbidity and temperature. As a result, South African estuaries represent a specialised environment[1] and of a total of approximately 1500 species of fishes found on the continental shelf, fewer than 100 species are able to make use of our estuaries.

The life cycle of most of these species involves the spawning by adults at sea, often close inshore and in the vicinity of estuary mouths. Egg and larval development also take place at sea, but there is a mass migration into estuaries by small juveniles when they are approximately 15 mm and upwards in length. This instinct for migration is very marked and during late winter, spring and early summer millions of fish fry enter estuaries, where the high temperatures and rich food supply favour rapid growth, and where they are also protected from most marine predators.[2-5] Juveniles spend varying lengths of time in estuaries, but generally migrate back to sea with the onset of adolescence, which often occurs at an age of about a year. These sub-adult fish tend to inhabit marine inshore areas, where they join the adult spawning populations once they become mature.[6] Adult fish increase in abundance seasonally when they enter estuaries to feed. At these times of the year they are readily accessible to sport anglers and constitute a valuable recreational and food resource[7-9] (e.g. during the famous grunter 'run').

From the foregoing it is obvious that the migration of fish in and out of estuaries is dependent upon each estuary being in contact with the sea, either through a permanently open mouth, or via a mouth which opens naturally at certain times of the year in response to seasonal rains and other enviromental factors. It is also clear that fish benefit from the rich feeding-grounds provided by estuaries, and that human disruption of this function can degrade estuaries to the point where they are of little value to fishes. Particularly significant are the submerged aquatic plants and the vegetation supported by the adjacent wetlands, both of which supply much of the plant detritus basic to the estuarine food web.[3,10-12]

How dependent are these fish on estuaries?

From research conducted in estuaries, biologists have long maintained that the most important role of this enviroment as regards fish populations is the provision of nursery grounds for juveniles. Recent studies have examined this role in more detail and have sought to show whether these fishes also utilize nursery grounds at sea. It is important to know this, because it tells us whether the survival of South African populations of these species is dependent on estuaries.

The search for nursery grounds at sea was concentrated on the Cape south and south-west costs, and supplemented by research in Natal. It involved sandy-beach seine net-

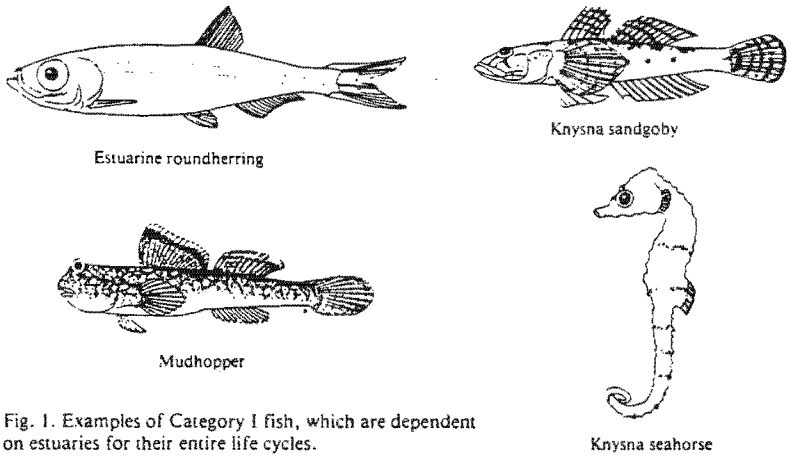

Fig. 1. Examples of Category I fish, which are dependent on estuaries for their entire life cycles.

Table 1. Fishes associated with South African estuaries.

Category I: *Truly estuarine species, dependent on estuaries for entire life cycle.*

Species	*Common name*	*Utilization*
Caffrogobius multifasciatus	prison-goby, tronk-dikkop	prey
Caffrogobius natalensis	baldy, kaalkop	prey
Clinus sp. nov.	Bot river clinid	prey
Gilchristella aestaurius	estuarine roundherring, rivier-rondeharing	prey
Gobionellus keiensis	Kei river goby	prey
Hippocampus capensis	Knysna seahorse, Knysna-seeperdjie	prey
Periopthalmus sobrinus	kingfin mudhopper, grootvin modderspringer	prey
Psammogobius knysnaensis	Knysna sandgoby, Knysna-sanddikkop	prey

Category II: *Species dependent on estuaries during juvenile phase of life cycle.*

Species	*Common name*	*Utilization*
Acanthopagrus berda	river bream, slimjannie	angling, food
Ambassis gymnocephalus	bald glassy, kaalkop-glasvis	prey
A. natalensis	slender glassy, slank glasvis	prey
A. productus	longspine glassy, langstekel-glasvis	prey
Caranx sexfasciatus	bigeye kingfish, grootoog-koningvis	angling, food
Chanos chanos	milkfish, melkvis	food, prey
Elops machnata	ten-pounder, tienponder, springer	angling, food
Hyporhamphus capensis	Knysna halfbeak, Knysna-halfbek	prey
Lichia amia	leervis	angling, food
Lithognathus lithognathus	white steenbras, witsteenbras	angling, food
Liza macrolepis	largescale mullet, grootskub-harder	food, prey
Monodactylus argenteus	Natal moony, Natalse maanvis	food, prey
M. falciformis	Cape moony, Kaapse maanvis	food, prey
Mugil cephalus	flathead mullet, platkop-harder	food, prey
Myxus capensis	freshwater mullet, varswaterharder	food, prey
Pomadasys commersonni	spotted grunter, spikkel-knorder	angling, food
Rhabdosargus holubi	Cape stumpnose, Kaapse stompneus	angling, food
R. sarba	Natal stumpnose, Natalse stompneus	angling, food
Terapon jarbua	thornfish, doringvis	angling, prey
Thyrssa vitrirostris	orangemouth glassnose, oranjebelglasvis	food, prey
Valamugil cunnesius	longarm mullet, langarm-harder	food, prey
V. robustus	robust mullet, wilde harder	food, prey

Category III: *Species whose juveniles occur mainly in estuaries, but are also found at sea.*

Species	*Common name*	*Utilization*
Carcharhinus leucas	Zambesi shark, Zambesihaai	angling, food
Gerres acinaces	smallscale pursemouth, kleinskubplooibek	food, prey
G. filamentosus	threadfin pursemouth, sweepvinplooibek	food, prey
G. oblongus	oblong pursemouth, langwerpige plooibek	food, prey
G. ovena	slenderspine pursemouth, slankstekelplooibek	food, prey
G. rappi	evenfin pursemouth, geïykvin-plooibek	food, prey
Hepsetia breviceps	Cape silverside, Kaapse spierinkie	prey
Heteromycteris capensis	Cape sole, Kaapse tongvis	prey
Liza alata	diamond mullet, diamant-harder	food, prey
L. dumerili	groovy mullet, keepharder	food, prey
L. tricuspidens	striped mullet, streep-harder	angling, food, prey
Ophisurus serpens	sand snake-eel	prey
Pomadasys hasta	javelin grunter, spies-knorder	angling, food
Pristis pectinata	largetooth sawfish, groottand-saagvis	angling, food
Rhabdosargus thorpei	bigeye stumpnose, grootoog-stompneus	angling, food
Scomberoides lysan	doubledotted queenfish, dubbelgekolde koninginvis	angling, food
Solea bleekeri	blackhand sole, swarthand-tongvis	prey
Sphyraena barracuda	great barracuda, groot barrakuda	angling, food
S. jello	pickhandle barracuda, piksteel-barrakuda	angling, food

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ting,[13] rotenone poisoning of intertidal rocky-pool ichthyofauna, near-shore sampling using beam trawls, try-nets and plankton nets, as well as SCUBA surveys of the ichthyofauna of sub-tidal reefs down to 30 m. In addition, a small-mesh trawling survey was conducted in the depth range 6 – 90 m between Algoa Bay in the east (33°53′S, 26°28′E) and St Sebastian Bay (34°06′S, 29°09′E) in the west.[14]

The inshore trawling survey revealed the occurrence of 12 species of estuarine-associated fishes over soft substrates and the SCUBA survey an additional four species over rocky bottoms on the Cape south coast.[14] These valuable new data together with the results of other near-shore research currently being prepared for publication, have enabled the authors to divide South Africa's fish fauna associated with estuaries into six categories according to the extent of

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Category IV: *Species whose juveniles occur mainly at sea, but are also abundant in estuaries.*

Species	*Common name*	*Utilization*
Argyrosomus hololepidotus	kob	angling, food
Arothron immaculatus	blackedged blaasop, swartrand-blaasop	prey
Caffrogobius nudiceps	barehead goby, blesdikkop	prey
Caranx ignobilis	giant kingfish, reus-koningvis	angling, food
Crenimugil crenilabis	fringelip mullet, fraiingbek-harder	food, prey
Diplodus sargus	blacktail, dassie	angling, food
Hemirhamphus far	spotted halfbeak, gevlekde halfbek	prey
Hilsa kelee	kelee shad, kelee-haring	prey
Johnius belengerii	minikob, mini-kob	prey
Leiognathus equulus	slimy, slymvis	prey
Liza richardsoni	southern mullet, suiderlike-harder	food, prey
Lutjanus fulviflamma	dory snapper,	angling, food
Omobranchus woodii	kappie blenny, kappie blennie	prey
Pelates quadrilineatus	trumpeter, trompeter	food, prey
Platycephalus indicus	bartail flathead, (river gurnard), balkstert-platkop	angling, food
Pomatomus saltatrix	elf	angling, food
Pranesus pinguis	hardyhead silverside, klipkop-spierinkie	food, prey
Rhabdosargus globiceps	white stumpnose, witstompneus	angling, food
Sarpa salpa	strepie	angling, food
Scomberoides commersonianus	largemouth queenfish, grootbek-koningvis	angling, food
Sillago sihama	silver sillago, silwer sillago	angling, food, prey
Stolephorus commersoni	tropical anchovy, tropiese ansjovis	prey
S. holoden	thorny anchovy, doring-ansjovis	prey
Syngnathus acus	longnose pipefish, langneus-pypvis	prey
S. djarong	belly pipefish, boepens-pypvis	prey
Tachysurus feliceps	sea catfish, seebaber	angling, food
Tylosurus leiurus	needlefish, naaldvis	angling, food
Valamugil buchanani	bluetail mullet, bloustert-harder	food, prey

Category V: *Species whose juveniles occur at sea, but sometimes stray into estuaries.*
Approximately 100 species of marine inshore fishes fall into this category.

Category VI: *Miscellaneous species not dependent on estuaries.*
(a) Freshwater species whose juveniles sometimes stray into estuaries. A total of 14 species fall into this group.
(b) Other species. A total of 11 species fall into this group. Some breed in both estuaries and fresh water (e.g. *Glossogobius giurus*, tank goby, tenk-dikkop; *Oreochromis mossambicus*, Mocambique tilapia, blou-kurper).

their dependence upon them. The species included in each category, their common names and an indication of whether they are utilized for angling, for human food or as prey by larger fish and bird predators, are set out in Table 1.

Category I comprises eight species which are dependent upon estuaries for their entire life cycles. Severe degradation of South African estuaries could threaten the extinction of these fishes in our waters.

These species are all small in size and include gobies, a mudhopper, a whitebait, and the Knysna seahorse (Fig. 1). Although of no direct significance for angling or food, they are eaten by predatory fish and birds. As a result they form an important part of the estuarine food web and losses in population or their extinction would have adverse ecological consequences. The reduced abundance of larger predatory angling fish in estuaries would be one such consequence.

Category II comprises 22 species which are dependent on estuaries during the juvenile phase of their life cycles and whose survival in South African waters is determined by the existence of ecologically viable estuaries along our coast. Angling fish in this category (Fig. 3) are the spotted grunter, white steenbras, leervis, ten-pounder, Cape and Natal stumpnoses, a kingfish and the river bream. These fish also constitute a valuable food resource, as do an additional nine non-angling species that include the milkfish and five species of mullet (Fig. 2). The remaining species are not directly exploited by man but are integral to the food web and are preyed upon by larger angling fish.

Category II also includes an additional four species that are dependent upon

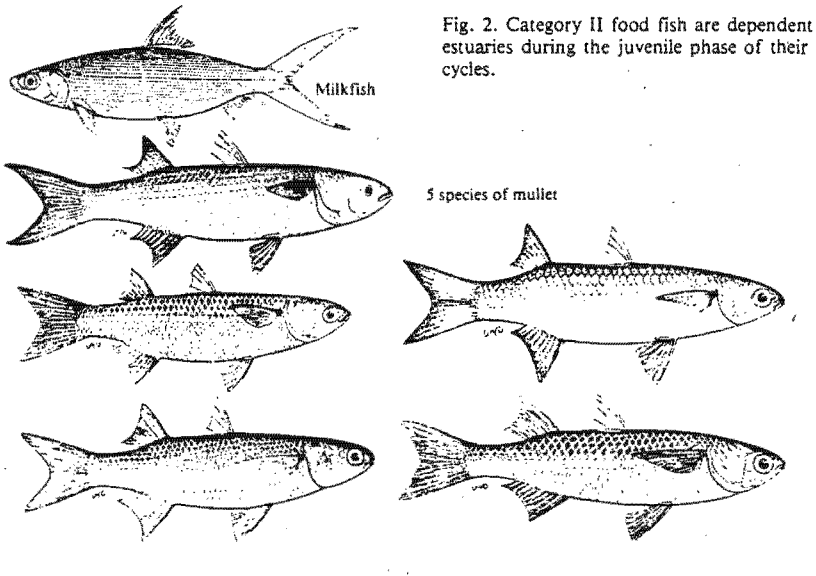

Fig. 2. Category II food fish are dependent on estuaries during the juvenile phase of their life cycles.

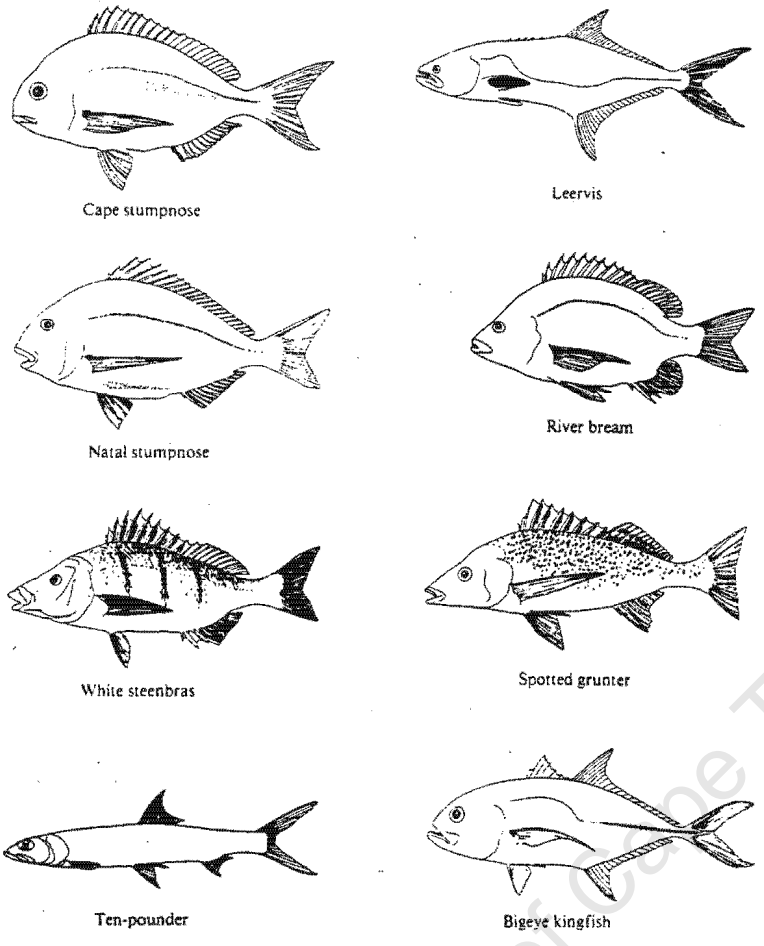

Fig. 3. Category II angling fish are dependent on estuaries during the juvenile phase of their life cycles.

estuaries for short periods during their life cycles. These are the freshwater eels, whose small elvers pass through estuaries in their migration from the sea into South African rivers, and which again occur in estuaries as adults during their migration back to sea to spawn (Fig. 4). The degradation of our estuaries would have serious consequences for these eel populations.

Category III includes 19 species whose juveniles are found mainly in estuaries but also at sea (Fig. 5). As a result these species are not entirely dependent on estuarine nurseries and, although they would survive in South African waters if extensive estuarine degradation occurred, their numbers would be drastically reduced. Angling species comprise a grunter, a stumpnose, a barracuda, a queenfish, a shark and a sawfish. Food fish include five species of pursemouth and three species of mullet, which are also taken by predatory fish and birds.

Category IV comprises 28 species whose juveniles are found mainly at sea, but are also abundant in estuaries. Although estuaries are not essential for their survival, these areas do make a contribution to the adult stocks because juveniles that grow up in estuaries migrate to sea to join the breeding populations.

Some of the better known angling species in this category are the kob, elf, blacktail, white stumpnose, giant kingfish and large-mouth queenfish. An additional 11 species are also of value as human food, while the remaining 11 prey species are not directly utilized by man.

Category V consists of approximately 100 species whose juveniles occur at sea and sometimes stray into estuaries. For these fish the estuarine environment is of no particular significance.

Category VI comprises 25 species which are associated with fresh water and whose juveniles are seldom found in estuaries. These areas are consequently of no significance to the survival of these fishes.

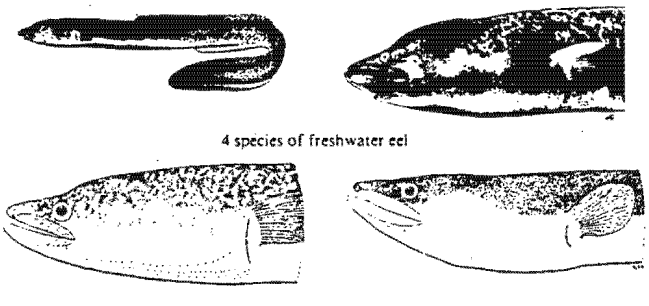

Fig. 4. Category II includes the eels which depend on estuaries when they migrate between South African rivers and the sea.

The above analysis of the dependence of fish on estuaries can be summarised as follows:

Category	No. of species	Relationship to South African estuaries
I	8	Dependent on estuaries during entire life cycle.
II	22	Dependent on estuaries during juvenile phase of life cycle.
	4	Dependent on estuaries during migration between rivers and the sea.
III	19	Largely, but not entirely, dependent on estuaries during juvenile phase of life cycle.
IV	28	Benefit from, but only partially dependent on, estuarine nursery areas.
V	*c.* 100	Stray into estuaries from the sea, not dependent on estuaries.
VI	25	Miscellaneous species not dependent on estuaries.

From this summary it is apparent that 81 species of fish are wholly or partially dependent on South African estuaries.

Discussion

Of the 81 species which depend on estuaries, 29 are taken by anglers and an additional 21 species are suitable for human food. Unfortunately, estuarine and marine inshore catch statistics for these species are not available, and the potential catch is also unknown. Consequently, we are unable to assess the value of the catch to the South African economy.

Equally important to consider is the rand value of activities associated with angling for sport in estuaries, such as the manufacture of boats, sales of outboard motors, fishing tackle, protective clothing and bait, the hire of accommodation, the sale of local real estate, and so on. Also relevant but even more difficult to quantify in monetary terms is the benefit of fishing as a healthy, outdoor recreational activity which provides relaxation and escape from the tensions of modern urban life.

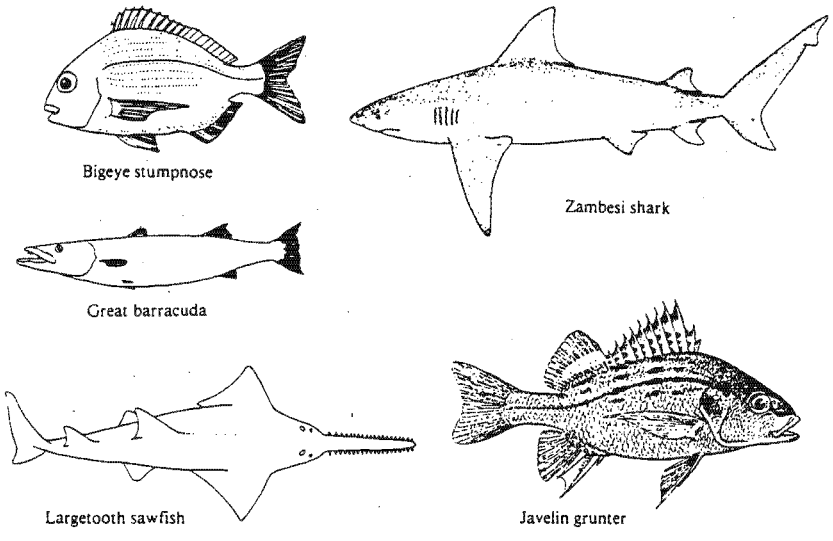

Fig. 5. Category III angling fish are largely dependent on estuaries during the juvenile phase of their life cycles.

Although it is not possible to place a value on these various factors, estuarine fish are undoubtedly of great significance to the national economy. Furthermore, as this resource is largely dependent on estuaries, it is in the national interest to manage estuarine systems so as to maintain their biological productivity and ecological diversity. This means that conservation of estuaries must be accorded a high priority when assessments are made of the merits of proposed development projects, many of which have quantifiable short-term benefits, but may cause degradation of the estuarine envionment and its fauna in the longer term.

The relevance of the above is emphasized by the fact that extensive degradation of South African estuaries has already taken place,[13,14] as a result of ignorance of and disregard for the consequences of man's activities in and around these sensitive systems. One common practice known to be detrimental to the fish fauna involves the artificial opening of estuary mouths, thereby interfering with the natural cycle of migration of juveniles into their nursery areas, and in their premature release to the sea. Another particularly detrimental practice involves encroachment onto wetlands adjacent to estuaries by agriculture, industry and transport systems, thus reducing the amount of plant detritus available to the base of the estuarine food web, and consequently reducing the size of the fish populations that can be supported. The impairment of normal tidal water exchange and the damming of flood waters by embankments and bridges also have adverse ecological consequences for estuaries, and consequently for their fishes.

We predict that if these and other forms of degradation continue there will be a continuing decline in the biological viability of South Africa's estuaries. The fish fauna will consequently become increasingly impoverished, it will provide less food and fewer opportunities for recreation for our growing population. The fishing tackle, boating, accommodation and real estate industries will also suffer.

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CHAPTER 9.

CHANGES IN THE FISH FAUNA OF THE BOT RIVER ESTUARY IN RELATION TO OPENING AND CLOSURE OF THE ESTUARY MOUTH

By

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SUMMARY

The fish community of the Bot River estuary was sampled with seine and gill nets between April 1980 and July 1983. During part of this period the estuary, which is usually closed, was in contact with the sea via an artificially opened deep-water mouth as well as the natural spillway into the adjacent Kleinmond estuary. This paper describes changes in the species composition, abundance and size-structure of the fish community that occurred as a result of these connections with the sea, as well as seasonal and longer-term changes that occurred during the closed phase. The implications of opening the mouth, for the fish and the fishermen that utilize the lagoon, are outlined and management options discussed.

INTRODUCTION

Work in South Africa and elsewhere has shown that the majority of fish species found in estuaries are of marine origin. Some of these species are able to complete their life-cycles in estuaries, but most may be classified as marine migrants (Gunther 1967, Wallace 1975, Day *et al.* 1981). Typically the migrant species spawn and complete their early stages of development in the sea. As juveniles they migrate into estuaries, where they remain for varying lengths of time before returning to the sea to spawn. This type of life-cycle has led to estuaries being termed 'nursery areas' and may have evolved because estuaries offer advantages over the marine environment in terms of increased protection from predators, calm, shallow waters and better feeding conditions (Blaber 1981, Day *et al.* 1981, De Decker & Bennett 1985). The reliance of juveniles of migrant species on estuarine nursery grounds varies considerably. Some species, such as the southern mullet *Liza richardsoni*, white stumpnose *Rhabdosargus globiceps*, and elf *Pomatomus saltatrix*, appear to use the favourable estuarine conditions opportunistically, juveniles also being very abundant in the sea. Others, like white steenbras *Lithognathus lithognathus*, Cape stumpnose *Rhabdosargus holubi*, leervis *Lichia amia*, and flathead mullet *Mugil cephalus*, are considered to be dependent on estuarine nursery grounds, and might be driven to extinction if denied access to these areas (Wallace *et al.* 1984).

The present paper focuses on the ichthyofauna of the Bot River estuary and, in particular, the import of mouth opening and closure on this fauna. The estuary is situated on the south-western Cape coast of South Africa. It is normally closed so that fish cannot migrate freely between it and the sea. During the past 60 years the sand-bar separating the estuary from the sea has been breached naturally on only two occasions

although it has been breached artificially at 2 to 4-year intervals during this period (Bally 1985). Conditions within the estuary vary markedly depending on whether it is open or closed and the amount of time that it has been isolated. Within a day of breaching, water-levels in the estuary drop from approximately 2,8 m to 0,4 m above mean sea-level, reducing the surface-area of the estuary by approximately 56% (Bally *et al.* 1985). The rapid decrease in water-area strands and kills most of the macrophytes in the lagoon (Bally 1985), resulting in the decimation of invertebrate populations (De Decker & Bally 1985) and the disappearance of most of the waterfowl (Heÿl & Currie 1985). After the initial outflow, the estuary becomes tidal and remains so until the end of the rains when outflow is insufficient to counter the bar-building effects of longshore drift. Once closed, water-levels may decline during the dry summer months, causing the estuary to become hypersaline but, at the onset of the winter rains, the estuary refills, salinities decline and a community typical of the closed phase begins to be re-established.

The reason that the Bot River estuary very rarely opens naturally is that the low-lying area between the western arm of the estuary and the adjacent Kleinmond estuary acts as a spillway or overflow (Fig. 1) which prevents water-levels in the estuary from becoming high enough to flow over the sand-bar and cut a channel into the sea. The overflow has a threshold level of approximately 2,3 m and it appears to operate most winters and during periods of heavy unseasonal rainfall. Since the threshold of the

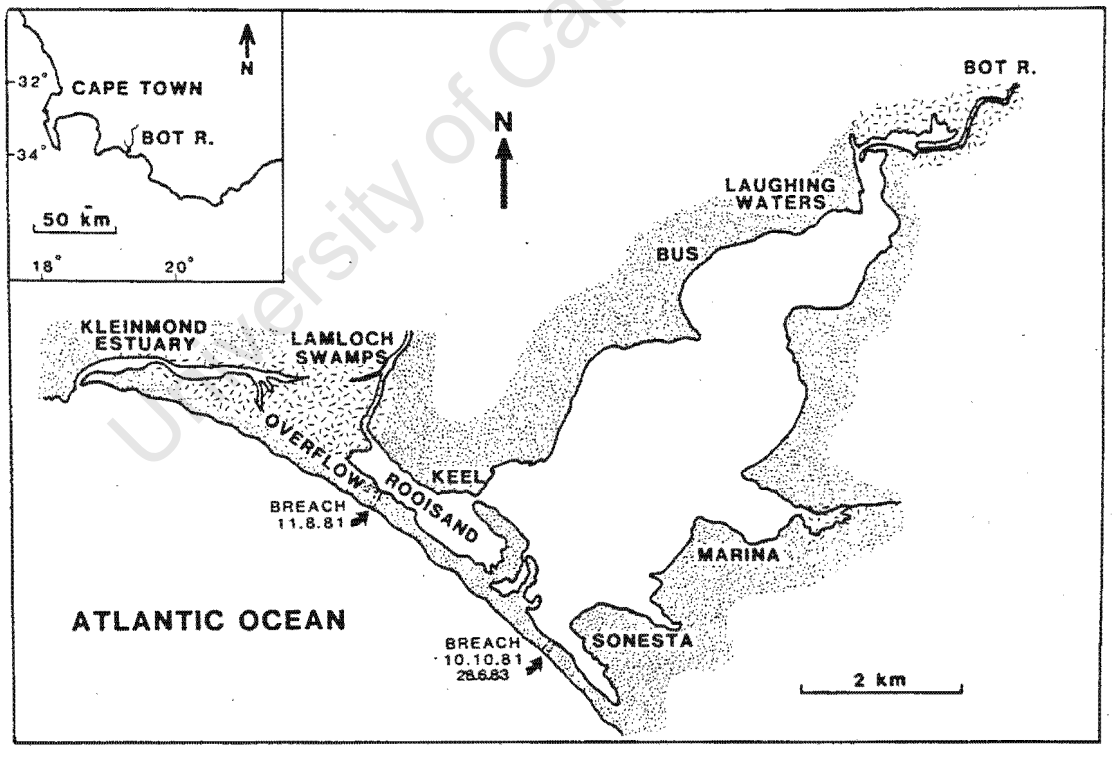

Fig. 1. The location of the Bot River estuary in the south-western Cape (inset) and the position of localities mentioned in the text.

spillway is above the level of the highest tides it does not allow saline water to enter the estuary. The effect of this overflow is therefore to decrease salinity in the lagoon.

The Bot River estuary is widely recognized as being a very productive fishing area. In the past the estuary has provided the sole livelihood of a number of fishermen (Stern 1983). Recently, however, commercial netting has been curtailed by the introduction of restrictive permits, but a large number of anglers still utilize the estuary. The question of how the estuary should be managed has arisen. One option is to continue periodic artificial opening, thereby continuing the widely fluctuating conditions that have been experienced in the estuary for at least the past 60 years. The other is never to open it artificially, in which case the estuary will evolve into the fresh-water lake that it might already have become but for human intervention. The purpose of this report is to describe changes in the fish community that occur in response to changing conditions in the estuary and, from these findings, to suggest a management strategy that will be most beneficial to the fish populations and to the fishermen that utilize the estuary.

METHODS

Two types of gear were used to sample the fish community: a seine net and a series of gill nets. The seine net (25 m long, 2 m deep, 10 mm stretched mesh) was laid parallel to the shore and hauled in on 30 m ropes, thus sampling an area of approximately 525 m^2. Hauls were made monthly at three localities, i.e. Laughing Waters, Bus and Die Keel (Fig. 1), between April 1980 and April 1981, and up to eleven hauls were made around the estuary in November 1981, January, April and August 1982, and July 1983 (Fig. 2). The fish caught were counted by species and all (or subsamples of 100 where catches of a species were large) preserved in 8% buffered formalin. Preserved fish were later measured to the closest millimetre (total length) and weighed to 0,01 g.

Multifilament gill nets were laid quarterly between April 1980 and August 1983.

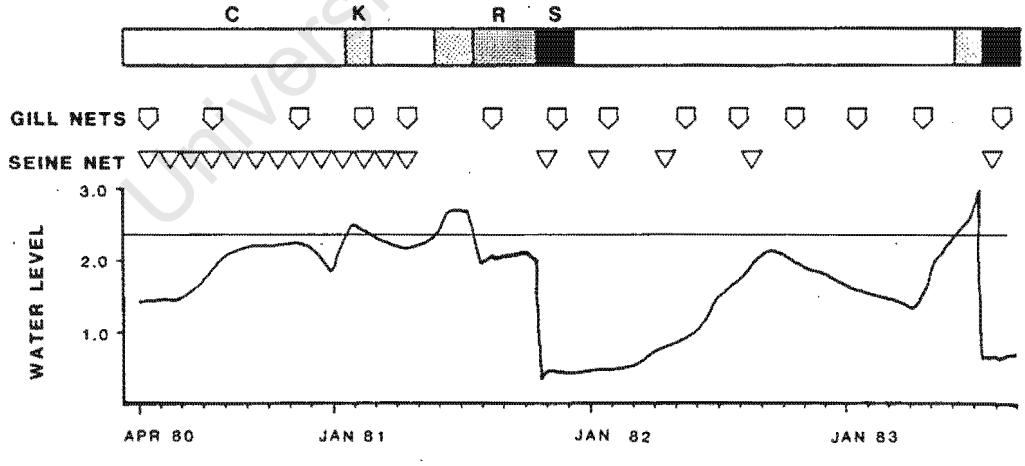

Fig. 2. The timing of gill and seine-net samples in relation to water-levels and state of the mouth of the Bot River estuary. C, K, R and S respectively indicate when the estuary was closed, or open to the sea via Kleinmond, Rooisand or Sonesta.

On each occasion three different localities, i.e. above Laughing Waters, off Die Keel and near the Marina (Fig. 1), were sampled on three consecutive nights. The nets were collectively 700 m long and 2,2 m deep, and consisted of seven separate 100 m panels each with a different mesh size (35, 45, 57, 73, 93, 118 and 150 mm stretched). All fish netted were counted, measured to the closest millimetre (fork length) and weighed to 1 g.

Sampling was timed to provide information on the structure of the fish community after approximately three years of isolation from the sea, and to monitor subsequent changes resulting from operation of the Kleinmond overflow and from the opening of a direct mouth near Sonesta.

RESULTS AND DISCUSSION

Water-levels and connection with the sea

Water-levels in the Bot River estuary between April 1980 and August 1983, the period during which the fish fauna was sampled, are shown in Figure 2. The typical seasonal cycle of increasing water-levels during the winter rainy season (May to August) followed by declines during the summer after the cessation of rainfall, is evident before December 1980 and between November 1981 and June 1983. This cycle is, however, complicated by unseasonable rainfall and artificial breachings of the dune barrier. Heavy rains in December 1980 and January 1981 caused a rapid increase in water-levels which resulted in a brief period of overflow to Kleinmond. The level then subsided only to increase, and overflow again, after the commencement of the normal winter rains. On this occasion levels rose above those normally experienced, causing inconvenience to some waterfront landowners and on 11 August the dune barrier was breached in the Rooisand area. This breach rapidly reduced the water-level to approximately 2 m above mean sea-level. Continuing rain during the period the Rooisand mouth was open caused salinities to decline until October when they became lethal to some of the fish species inhabiting the estuary. On 10 October the dune barrier was again breached, this time at the traditional site near Sonesta, to allow saline water to penetrate the estuary, causing a massive reduction of water-level. The estuary then closed again early in December due to a building-up of the sand-bar across the mouth, and its level gradually rose during the following winter. Artificial breaching again took place at Sonesta in June 1983, with a similar rapid reduction of level and volume (Fig. 2).

The fish community

Marked differences are apparent in the species composition and abundance of catches made with the seine and gill nets. Over 90% of the seine net catch comprised small species which seldom exceed 100 mm in length, whereas the gill net catch consisted mainly of larger species, most individuals being in excess of 200 mm. These differences are a reflection of the smaller mesh size of the seine net coupled with the fact that only small fish are common in the shallows sampled by the seine net.

Seine-net samples

A total of 99 238 fish representing 14 species was caught with the seine net (Table 1). The six small species which breed in the estuary were taken in almost every haul and accounted for 97% of all the fish caught. Cape silversides *Hepsetia breviceps* (65%), and estuarine round herrings *Gilchristella aestuarius* (15%), both small shoaling species, were numerically dominant. The only common marine migrant was *Liza richardsoni*, which comprised 2,8% of the total catch. The five other migrants occurred sporadically, providing only 0,2%, and fresh-water species made up only 0,02% of the total number of fish caught.

Overriding this general pattern, changes in the species composition and relative abundance did occur and can be attributed to changing water-levels in the estuary and the type and timing of connection with the sea. A comparison of the average of monthly samples taken between April and December 1981, after approximately 3 years of closure, with those between January and April 1981, i.e. during and immediately after overflow to Kleinmond (Table 1), allows assessment of the importance of the overflow as a migratory route. The six small species which breed in the estuary dominated catches during both periods. Together they accounted for 99% of the total number of fish caught and their relative contribution to the samples was similar each month. The two- to threefold increase in numbers of *H. breviceps, G. aestuarius, Psammogobius knysnaensis* and *Caffrogobius multifaciatus* after December represents a seasonal increase in abundance, not immigration.

In contrast the 76-fold increase in numbers of *L. richardsoni*, a species which does not breed in the Bot River estuary or in estuaries elsewhere (Day *et al.* 1981, Wallace *et al.* 1984), occurred because this species entered into the estuary from the sea via Kleinmond. Evidence for this is provided by the fact that all the *L. richardsoni* caught before January 1981 were 120 mm or larger and therefore more than a year old (Ratte 1976) whereas those caught between January and April were mainly between 40 and 60 mm, i.e. less than a year old.

Four other marine migrant species were caught between April 1980 and April 1981. The eight *Mugil cephalus* caught in June 1980 were between 115 and 201 mm long. No detailed age study of South African populations of this species has been published but Day *et al.* (1981) and Van der Elst (1981) indicate that these individuals would be less than two years old. The single *Rhabdosargus holubi* caught in April 1980 was 116 mm and approximately two years old (Blaber 1974). Both these species must therefore have entered the estuary after it closed in 1978, the most likely route being via Kleinmond, since this connection was open during the rainy season in 1978 and 1979. The very low numbers of those two species and their absence from samples taken after January 1981 suggests, however, that the Kleinmond route is not of great importance in allowing their recruitment. Published information on the age–length relationships of *Lithognathus lithognathus* (Mehl 1973) and *Lichia amia* (Blaber 1974) suggests that the specimens of these two species were sufficiently large to have entered the estuary in 1977 when it was last open directly to the sea. On the basis of the abundance and size-structure of the marine migrant species sampled, it therefore appears that the

Table 1

Species composition and abundance of catches made with a small-mesh seine net around the shallow margins of the Bot River estuary during the period April 1980 to July 1983. Each species is classified according to whether it breeds in estuaries (B), is a marine migrant (M) or is of fresh-water origin (F). Abundance is expressed as the average number of fish caught per haul (approx. 525 m²) on each occasion.

Species		1980 APR–DEC closed	JAN–APR overflow	1981 NOV open	JAN closed	1982 APR closed	AUG closed	1983 JUL open	Total catch	% N
Hepsetia breviceps	B	560,4	1 665,7	649,6	975,0	868,6	735,0	416,9	64 490	65,0
Gilchristella aestuarius	B	137,4	287,3	321,2	92,5	129,3	43,3	321,7	14 913	15,0
Psammogobius knysnaensis	B	16,6	48,6	146,8	181,3	23,7	78,3	228,9	7 105	7,2
Caffrogobius multifasciatus	B	1,0	2,0	102,8	76,3	86,6	1,0	433,7	7 071	7,1
Liza richardsoni	M	0,4	31,2	89,2	75,0	38,4	7,3	55,7	2 801	2,8
Clinus spatulatus	B	24,4	3,6	29,6	67,5	37,1	16,7	0,5	1 905	1,9
Syngnathus acus	B	4,4	3,2	7,6	1,8	3,6	2,7	45,8	794	0,8
Mugil cephalus	M	0,3	0,1	7,3	1,0				91	0,1
Lithognathus lithognathus	M	0,6	0,8		0,3	0,1			27	<0,05
Oreochromis mossambicus	F	0,1	0,1					0,9	13	<0,05
Cyprinus carpio	F		0,3					0,5	9	<0,05
Hyporhamphus knysnaensis	B?	<0,05	0,4			0,3			8	<0,05
Lichia amia	M	0,1			0,1	0,3			6	<0,05
Rhabdosargus holubi	M	<0,05			0,4	0,1			5	<0,05
No. of fish per haul		248,6	681,1	1 264,1	1 471,2	1 188,1	884,3	1 504,6	99 238	
No. of species		6	9	8	11	11	7	9	14	
No. of hauls		27	12	10	8	7	6	11	81	

Kleinmond connection is a significant avenue of recruitment only for *L. richardsoni*, other species apparently not using it to any great extent.

The species composition and abundance of fish in seine-net samples taken in November 1981 and June 1983, while the mouth was open, and in January, April and August 1982, after the mouth had closed and water-levels were rising, are shown in Table 1, and allow an assessment of changes in the fish fauna which are due to the opening of the mouth. Knysna sand gobies *Psammogobius knysnaensis*, prison gobies *Caffrogobius multifasciatus*, and *Gilchristella aestuarius* were all most abundant when the mouth was open. These species are entirely dependent on estuaries, being very rare in the marine environment (Wallace *et al.* 1984), so it is unlikely that migration can explain the increased catches. It is possible that population sizes were actually unchanged, since the reduction in volume of the estuary that occurs when it is opened would have concentrated these species, thereby increasing their densities. Another factor contributing to increased catches during the open phase is that the seine net was probably more efficient over the sparsely weeded substrata than in the dense macrophyte beds that were present after the estuary had been closed for some years. Declining catches of these species after closure can probably be attributed to the increasing volume of the estuary and the re-establishment of aquatic macrophytes.

The abundance of *H. breviceps* did not vary appreciably with changing water levels. Since the factors contributing to the increased abundance of the other species must also apply to *H. breviceps*, it appears that there were fewer *H. breviceps* in the estuary after it opened. This species is not strongly estuary-dependent since it is also abundant in the sea. Thus it may be assumed that large numbers emigrated from the estuary while the mouth was open.

Liza richardsoni was most abundant when the mouth was open but numbers declined after closure. During November 1981 and July 1983 most individuals were between 30 and 60 mm in length, a size suggesting recent recruitment. More individuals appear to have entered the estuary in November than in July, possibly because there may have been a greater number of potential recruits in the inshore marine area in November. Recruitment in July may, however, have been retarded by colder water and stronger outflowing currents at that time. Declining catches after November 1981 may be attributed to the increasing volume of the estuary and decreasing net efficiency, coupled with mortality and movement of large individuals into deeper water.

Very few other marine migrants were sampled between November 1981 and July 1983 (Table 1). All those caught were very small, which suggests that they had entered through the recently opened mouth. Seventy-three *Mugil cephalus* were sampled in November but none the following July. A combined total of only ten individuals of *Lithognathus lithognathus, Lichia amia* and *Rhabdosargus holubi* were sampled, all in January and April 1982. These species possibly entered the estuary after the November sampling and it seems likely that recruitment would have been stronger had the estuary remained open further into the summer.

Gill-net samples

9 421 fish representing 23 species were taken in the gill nets between April 1980 and August 1983 (Table 2). Over 99% of the total sample were marine migrants with *Liza richardsoni* and *Lithognathus lithognathus* the two most important species in terms of both number and biomass. *Caffrogobius multifasciatus* (40 individuals) was the only species that breeds in the estuary. The three fresh-water species together contributed only 20 individuals.

The number and biomass of the combined catch on each sampling occasion are shown in Figure 3. Before the Kleinmond overflow became operative the numbers of fish caught were relatively stable at between 230 and 400 per sample. When the overflow became operative and, more particularly, when the mouth was opened at Sonesta in October 1981 the catch increased dramatically until January 1982 when over 2 000 fish were taken. Thereafter both numbers and biomass declined.

Liza richardsoni, being the most abundant species (74% of total numbers and 40% of biomass), had a marked effect on these trends. The number, biomass and average length of this species in each sample are shown in Figure 4. While the estuary was closed the number of fish caught remained almost constant, while biomass and mean length increased, representing growth over the period. After the Kleinmond overflow became operative catches increased, but the mean size of the fish declined, indicating that small fish were entering the estuary. Catches continued to increase throughout 1981, most strikingly after the mouth was opened, while the mean size decreased, thus recruitment continued throughout this period. The largest catch was made in January 1982, a short while after the estuary had closed. The average length of the fish continued to decline until July 1982. This decline represents continuing recruitment into the catches of fish that were previously too small to be taken with the mesh sizes used. Only after July 1982, when the majority of the fish had reached catchable size, did average lengths increase, further recruitment into the estuary being impossible since both the Kleinmond overflow and the mouth were closed. After the mouth was opened again in June 1983, numbers increased slightly but not nearly as much as after the October 1981 opening.

Before considering the characteristics of the other important species populations, a mass mortality that occurred in October 1981 should be mentioned since, although it had little effect on *Liza richardsoni*, it has a bearing on the relative abundance of the other species. The fish were killed by low salinities which occurred after the dune barrier was breached in the Rooisand area. This breaching had a similar effect to the Kleinmond overflow in that it allowed estuarine water to escape but prevented any influx from the sea. Salinities therefore declined rapidly. Details of the species and numbers of fish to have died are given in Bennett (1985). Judging from the numbers present in the preceding gill-net samples, some species such as *Liza richardsoni, Mugil cephalus* and *Lichia amia* were unaffected by the low salinities, whereas others like *Galeichthys feliceps, Rhabdosargus globiceps, Lithognathus lithognathus* and *Pomatomus saltatrix* died in relatively large numbers. Since no sample was taken between the mortality and the subsequent opening of the mouth at Sonesta the effects of this

Table 2

The species-composition and abundance of gill-net catches made in the Bot River estuary between April 1980 and April 1983. The species are classified according to whether they breed in estuaries (B), are marine migrants (M) or are of fresh-water origin (F). Abundance is expressed as the total number of fish caught over three consecutive nights in a 700 m net with seven 100 m panels of different mesh-sizes.

		1980				1981			1982					1983					
		APR	JUL	NOV	FEB	APR	AUG	NOV	JAN	MAY	JUL	OCT	JAN	APR	AUG				
Species	Class	closed	closed	closed	over-flow	closed	over-flow	open	closed	closed	closed	closed	closed	closed	open	Total Catch	% N	Mass Kg
Liza richardsoni	M	59	103	95	101	109	375	472	1 849	472	495	1 122	462	479	657	6 850	73,7	1 491
Lithognathus lithognathus	M	30	114	25	113	159	115	1	28	50	48	2		27	6	718	7,6	950
Galeichtys feliceps	M	66	65	81	65	77	188	16	33	8	9		17	16	15	656	7,0	200
Mugil cephalus	M	33	37	1	31	25	14		35	31	31	82	11	56	10	397	4,2	230
Pomatomus saltatrix	M	9	2	2	6	3	1		56	93	36	64	61	37	3	373	4,0	308
Lichia amia	M	22	14	12	32	26	8	19	17	23	9	3	6	4	4	199	2,1	476
Rhabdosargus globiceps	M		4	33		1	2					1	1	1		32	0,5	16
Caffrogobius multifasciatus	B			1	4	1	21	12				1				40	0,4	1
Trigla capensis	M									15	6	6	4	4		35	0,4	8
Trachurus capensis	M		1		2				8	2	8	2	1			23	0,2	4
Rhabdosargus holubi	M		1	9	5	1	5									21	0,2	12
Cyprinus carpio	F	1			5	3	3					5				17	0,2	17
Monodactylus falciformis	M	4			2	4		3					3			16	0,2	3
Sarpa salpa	M				12											12	0,1	5
Pomadasys olivaceum	M	4		2	1											7	0,1	1
Diplodus cervinus	M	1	2			1										4	<0,05	2
Micropterus salmoides	F				2											2	<0,05	<0,5
Solea bleekeri	M				1		1									2	<0,05	<0,5
Liza tricuspidens	M				2											2	<0,05	<0,5
Rhinobatus annulatus	M									1						1	<0,05	1
Engraulis capensis	M									1						1	<0,05	<0,5
Oreochromis mossambicus	F	1														1	<0,05	<0,5
Diplodus sargus	M		1													1	<0,05	<0,5
Total no. of fish		230	344	261	384	410	733	523	2 026	695	642	1 288	565	624	695	9 421		3 734
No. of species		11	11	10	16	12	11	6	7	10	8	10	9	8	6			

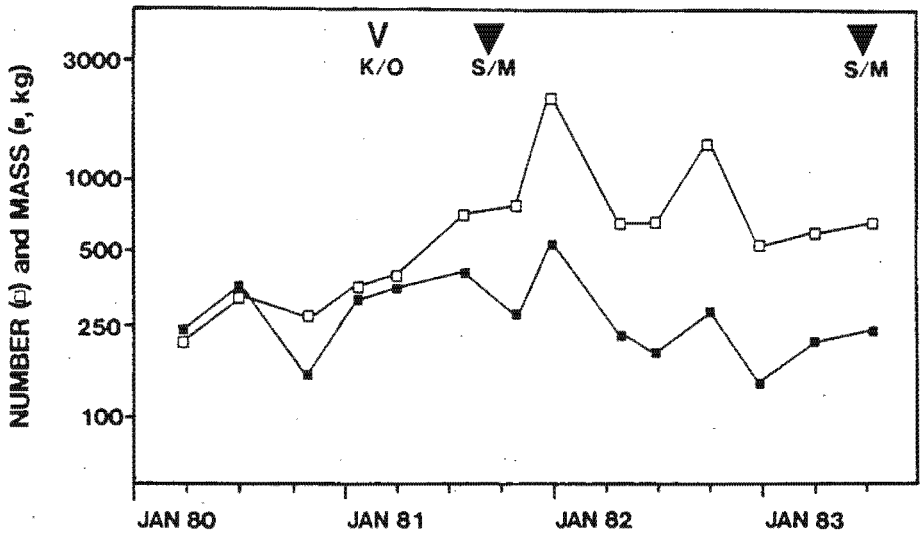

Fig. 3. The total number and biomass of all species captured in gill-net samples between April 1980 and April 1983. K/O and S/M show when the Kleinmond overflow and direct mouth at Sonesta were opened.

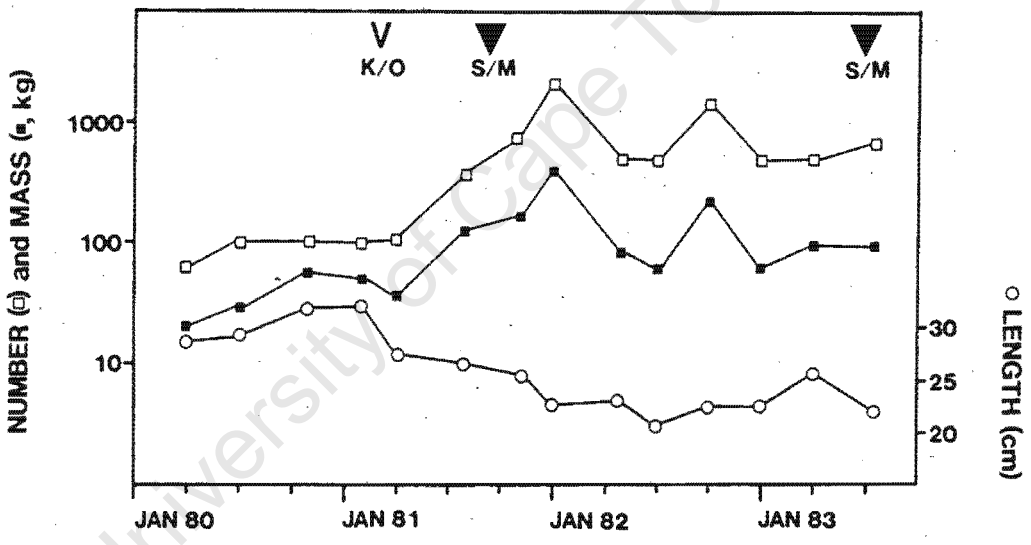

Fig. 4. Total number, biomass and average length of *Liza richardsoni* taken in gill nets between April 1980 and April 1983. K/O and S/M show when the Kleinmond overflow and direct mouth at Sonesta were opened.

mortality on the whole fish community could not be ascertained. Decreased numbers in the November sample, of species known to have been killed, may therefore reflect a population reduced by the mortality, by emigration through the open mouth or by a combination of these two factors.

Lithognathus lithognathus was the second most important species recorded in the gill nets, although its contribution to the catches was highly erratic (Fig. 5). Prior to the mouth-opening in November 1981, the number of fish caught remained relatively stable and average size increased. Only one individual was caught in November, after the

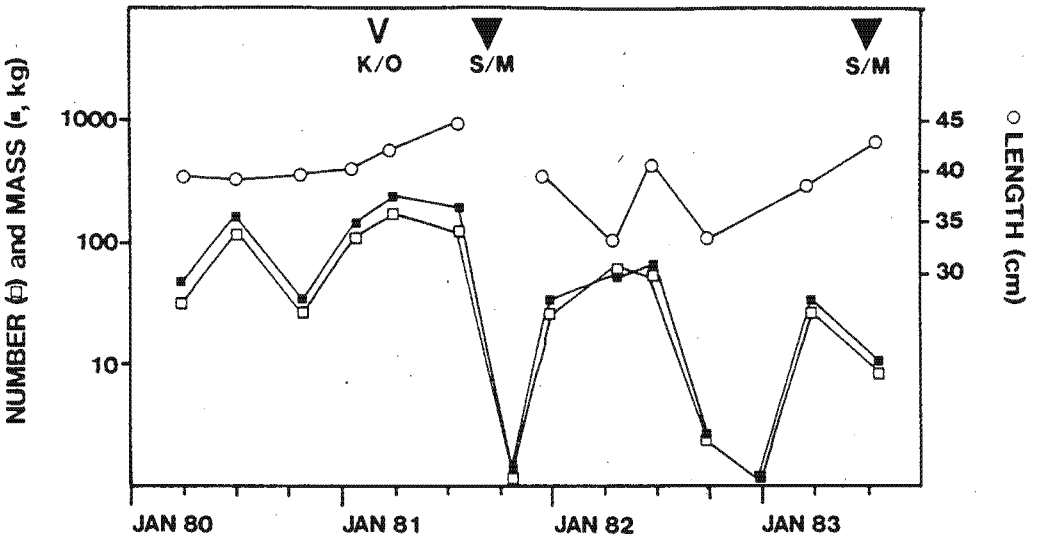

Fig. 5. Total number, biomass and average length of *Lithognathus lithognathus* taken in gill nets between April 1980 and April 1983. K/O and S/M show when the Kleinmond overflow and direct mouth at Sonesta were opened.

mouth was opened, suggesting that the population had been reduced by the preceding hyposaline conditions and/or migration out to sea. Catches in January 1982 and the two following sampling periods were somewhat improved, and included a small population of fish too small to have been in the estuary since it was previously opened in November 1977. Numbers were erratic thereafter, but since catches after the mouth opened were never as good as those made during the preceding closed phase, it appears that recruitment was poor. When the mouth was opened in June 1983 the numbers dropped again, in a manner similar to that after mouth-opening in October 1981 (Fig. 5).

Pomatomus saltatrix clearly illustrates the trends in abundance and size-composition expected of a marine migrant species in a closed estuary (Fig. 6). Few individuals remained in the estuary after almost four years of closure, and all were large fish which, according to Van der Elst (1976), were approximately five years of age. These fish therefore probably entered the estuary in 1977 as one-year-olds. No *P. saltatrix* were caught in November 1981 when the mouth was open, possibly because all the large fish had emigrated, or been killed by the low salinities, and new recruits had either not yet entered or were too small to be sampled. Good catches of small fish in January and May 1982 showed that strong recruitment had occurred by this time. Numbers declined thereafter while biomass and mean length increased. The mouth opening of June 1983 resulted in a substantial decline in numbers as the large fish emigrated. By August 1983 there had not yet been any recruitment of young fish.

Lichia amia followed a very similar trend to that described for *P. saltatrix*. Catches prior to November 1981 consisted entirely of large fish, whereas those after that time were a mixture of large fish, which had probably remained in the estuary, and small ones which recruited while the mouth was open. This species, however, was more abundant before the mouth opened in November 1981 and since none were observed to

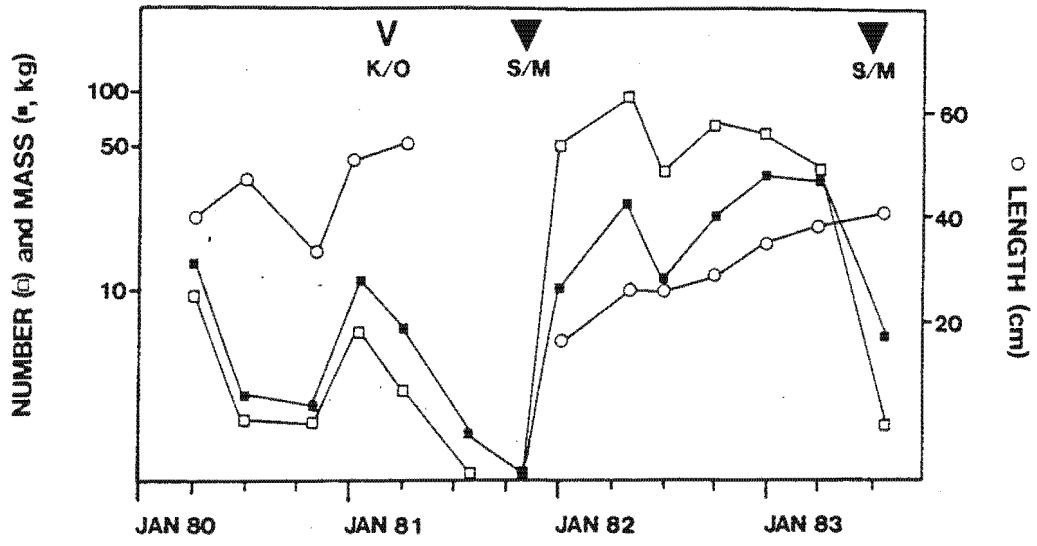

Fig. 6. Total number, biomass and average length of *Pomatomus saltatrix* taken in gill nets between April 1980 and April 1983. K/O and S/M show when the Kleinmond overflow and direct mouth at Sonesta were opened.

have been killed by low salinities, emigration probably exceeded recruitment. Too few fish were captured after the June 1983 opening to comment about changes of population structure.

The size-structure and abundance of *M. cephalus* is not readily interpretable. Before the November 1981 opening, individuals less than two years old appeared in the catches, confirming that this species is recruited via Kleinmond. Gill-net catches after November 1981 (Table 2) showed *M. cephalus* to be generally more abundant in the estuary after the mouth was opened in October 1981, but reduced in number after the opening of June 1983. Conversely, considerably fewer *Galeichthys feliceps* occurred in catches after the mouth opened in October 1981 (Table 2), possibly reflecting the large proportion of the population that succumbed to the preceding low salinities. Recruitment was apparently poor, only a few small individuals being recorded after the mouth had opened. No decline in numbers followed the opening in 1983, which was not preceded by lethally low salinities.

Small or variable sample sizes and/or slow rates of growth make the observed changes in the abundance and size-structure of some of the remaining species difficult to interpret. Nevertheless it is tempting to suggest that the rarity or absence of species such as *Rhabdosargus globiceps, R. holubi, Solea bleekeri* and *Liza tricuspidens*, after the estuary was first opened (Table 2), was the result of emigration and poor recruitment. Conversely gurnards *Trigla capensis*, maasbankers *Trachurus capensis*, sandsharks *Rhinobatus annulatus*, and anchovies *Engraulis capensis*, species which are not normally considered 'estuarine', were more abundant or occurred in the estuary only after the mouth had opened in October 1981. These species were trapped in the estuary when the mouth reclosed and would be expected to survive only until salinities fell to lethal levels. None was recorded after the June 1983 opening.

CONCLUSIONS

During the period of sampling the Bot River estuary gained contact with the sea via three routes—the Kleinmond overflow, the breach at Rooisand and the direct, artificially opened mouth near Sonesta. The impact of the Rooisand breach was to lower both water-levels and salinities while failing to allow sea-water to enter the estuary. It therefore hastened the mortality of fish (Bennett 1985) which was in any case probably impending because of the unseasonable flood which occurred at that time, but it failed to allow any recruitment.

The Kleinmond overflow was a significant avenue of recruitment only for *Liza richardsoni* although a few other migrant species used it to a limited extent.

The responses of the different species to direct opening of the estuary at Sonesta depended largely on their life-cycles. With the exception of *Hepsetia breviceps* and *Syngnathus acus*, species which breed in the estuary did not emigrate when it was open. This finding lends support to the conclusion reached by Wallace *et al.* (1984) that *Gilchristella aestuarius, Psammogobius knysnaensis, Caffrogobius multifasciatus* and *Clinus spatulatus* are entirely dependent on estuaries throughout their life-cycles.

The abundance and size-structure of those species which breed only in the sea showed a common pattern. Typically, only large individuals of these species were present before the estuary was opened. After opening, catches of the large fish declined while small fish suddenly appeared, often in large numbers. Once the estuary reclosed, numbers decreased due to mortality and average length and biomass increased due to growth. Fish that clearly fitted this pattern were *Pomatomus saltatrix, Lichia amia, Lithognathus lithognathus* and *Liza richardsoni*, all euryhaline marine species which use estuaries as nursery grounds (Wallace *et al.* 1984).

There are two very important considerations relating to the management of the Bot River estuary. Firstly, all the species of importance to sport and net fishermen are marine migrants. Their cycles of abundance and size-structure make it clear that periodic breaching of the dune barrier is essential for these species to remain available to fishermen in the estuary. It is also apparent that the quality of the fishing owes much to the fact that the estuary remains closed for extended periods, allowing the fish to become larger than they do in estuaries that are in more frequent contact with the sea. The second important factor is that some of the fishing species, such as *Lithognathus lithognathus, Lichia amia, Mugil cephalus* and *Rhabdosargus holubi*, may be entirely dependent on estuaries as juveniles (Wallace *et al.* 1984). Since the Bot River estuary is the third-largest estuarine area in the Cape Province it may play a significant role in maintaining stocks of these species.

If the estuary were never to be opened it would probably become a fresh-water lake within a few years (Branch *et al.* 1985). If salinities decline most marine species will die out as their lethal limits are reached (Bennett 1985, Whitfield *et al.* 1981). Experience has shown that low-salinity and fresh-water coastal lakes that have historical connections with the sea predominantly support fresh-water species, and that exotics such as *Cyprinus carpio* and *Micropteris salmoides* often become abundant. The only marine species to remain in the Bot River estuary, should it become a fresh-

water system, would be *G. aestaurius* and *H. breviceps*, which have survived in other low-salinity lakes such as Groenvlei (Ratte & Hanekom 1980) and Lake Sibaya (Allanson *et al.* 1974).

Accepting that the Bot River estuary needs to be opened artificially if fishermen and estuary-dependent fish are to benefit, consideration must be given to the timing and location of the breach and to the duration of the closed phase.

More recruits were found to be present in catches in the two to three months after the October 1981 opening than after the July 1983 opening (Tables 1 & 2), suggesting that the estuary should be opened in summer. Additional support for this conclusion comes from records of recruitment into the nearby Palmiet and Kleinmond estuaries (Bennett, unpublished data), where recruitment was strongest between November and March. Data on the spawning seasons of some of the migrant species found in the Bot River estuary are summarized by Day (1981) and Van der Elst (1981). These show that, although most species have extended spawning seasons, peak activity is usually in the spring and early summer months (August to November). Most recruits will therefore be available in the summer. Opening the mouth in the dry summer months may, however, not be ideal, since river input is reduced and water-levels in the estuary are lower. When opened, the outflowing water may not cut a channel sufficiently deep to remain open for more than a short time. The best time to open the estuary would therefore be in early summer before water levels have declined, probably October or November in most years.

The frequency of opening presents a problem because of the opposing requirements of the estuary-dependent fish and the fishermen. To function optimally as a nursery area, the estuary should be open every year to accommodate the juveniles which are spawned annually but, to remain attractive to fishermen, it should remain closed long enough for the fish to become larger than they are in other local estuaries.

Available knowledge of salinity tolerances, mortality rates and the ages at which the migrant species become mature, enables an evaluation of the maximum period that the estuary should remain closed. Salinities decline while the mouth is closed and when they reach approximately 4‰ many of the euryhaline marine migrants start to die (Bennett 1985). When the October 1981 mortality occurred it had taken four years for salinities to reach lethal levels. The decline in salinity during this period was accelerated by unseasonable rains in January 1981 and the opening of the mouth in the Rooisand area. It may therefore be expected that mass mortalities will occur after approximately four or five years of closure.

Mortality due to other factors occurs throughout the closed period and gill-net catches give an idea of the rates. In 1977 Ratte (1978) sampled the estuary while it was open. When his catches are compared with the average catch between April 1980 and April 1981, it seems that the number of fish in the estuary had declined by 70%. Mortality rates may, however, be very variable since a decline of similar magnitude was recorded over only 15 months after the 1981 opening. The effect of this decline on fishing is unknown but, despite the fact that the biomass of individual fish is increasing, it is probably detrimental. Also unknown is whether this mortality rate is greater or less than that experienced by the same species of fish (of equivalent size) in the sea. What is

clear, however, is that if mature fish are prevented from returning to the sea, the reproductive output of the species will be reduced. The approximate ages of maturity of the species of interest in this study are known, or can be estimated from published information. *Pomatomus saltatrix* begin to mature at two years of age (Van der Elst 1976), *Rhabdosargus globiceps, R. holubi* and *Liza richardsoni* mature in their third year (Talbot 1955, Blaber 1974, Lasiak 1983), *Mugil cephalus* and *Lichia amia* in their fourth (Van der Elst 1981) and *Lithognathus lithognathus* take five or more years to mature (Mehl 1973). If there is to be no loss of reproductive output due to the confinement of these species in the estuary it should be opened approximately every three years.

There does not appear to be any justification for opening the estuary more frequently than this, unless it can be shown that potential recruits which have been spawned at sea cannot be accommodated in other nearby estuaries when the Bot River estuary is closed, or that the mortality of subadult fish in the estuary is appreciably greater than it is in the sea. However, considering that it is only through human interference that the estuary is available to marine migrant fish, and that frequent opening would adversely affect the quality of fishing, this seems unjustified. Artificial breaching of the dune barrier at Sonesta, during the early summer at 3 to 4-year intervals, (or at any time salinities fall below approximately 5‰) is suggested as the management strategy best suited to the conservation of estuary-dependent fish in the south-western Cape and to the needs of the fishermen who utilize the Bot River estuary.

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CHAPTER 10.

A MASS MORTALITY OF FISH ASSOCIATED WITH LOW SALINITY CONDITIONS IN THE BOT RIVER ESTUARY

By

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SUMMARY

The Bot River estuary remains closed for prolonged periods, during which the salinities decline progessively. In October 1981, after four years of isolation from the sea, the maximum salinity in the estuary fell to 3‰ resulting in a mass fish mortality. The extent of this is compared with the species composition and relative abundance of fish prior to the mortality and with published records of the minimum salinities these species were previously known to tolerate.

INTRODUCTION

Estuaries are characterized by extensive changes in salinity and temperature. These changes may occur rapidly in response to tides and floods, seasonally, or over longer periods if the estuary is isolated from the sea. It is unusual for changes of equivalent magnitude to occur in the sea, but when they do, massive mortalities of marine life may result (Brongersma-Sanders 1957, Smith 1965).

Most estuarine fishes are of marine origin, and have evolved adaptations that enable them to survive much of the environmental variation that occurs in estuaries (Lockwood 1976). Very little is known of the tolerance limits of South African estuarine fish to fluctuations of salinity, but records of distribution, such as those presented by Whitfield *et al.* (1981), show that not all species found in estuaries are adapted to the same extent.

Many South African estuaries are closed for much of the year due largely to the strongly seasonal rainfall pattern. After the onset of the rains water-levels rise and sandbars isolating the estuaries from the sea are breached. These estuaries then remain open and tidal until freshwater input is insufficient to counteract the bar-building tendency of longshore drift. Once an estuary has closed, salinities sometimes increase due to evaporation. More often, however, salinities decline as a result of seepage of saline water through the sandbar and the maintenance of some river flow. Considering the frequency of droughts, unseasonal rainfall, and the incidence of dam-building and water-extraction in the catchment areas of South African estuaries, it is surprising there are so few documented cases of fish mortalities caused by extreme salinities.

Wallace (1975b) has recorded the fish fauna that occurs in Lake St Lucia during hypersaline conditions (60–110‰). He notes that the fish were considerably less diverse than under more normal conditions but that very few dead fish were observed, indicating migration into less saline areas. Blaber (1981) has described a mass mortality of a freshwater species, *Clarias gariepinus*, the result of high salinities induced by unusual wind conditions. He also reports an observation by Taylor that the same species was killed by being washed into high salinity waters (42‰) by sudden flooding of the Mkuze River. A major mortality caused by low salinities occured in Lake St

Lucia between May and July 1976, when exceptionally heavy rains caused salinities over the entire system to fall to between 3,5‰ and 1,0‰ (Blaber & Whitfield 1976). These low salinities, in conjunction with low temperatures (12°C), apparently caused the death of approximately 100 000 fish of 10 species. All the species that died were of marine origin and none had previously been recorded in salinities below 7‰. The only other published record of a mass fish mortality attributable to low salinities in a South African estuary is the observation by G. Jackson, cited by Blaber and Whitfield (1976), that numbers of *Pomadasys commersoni* were found dead in Lake Nhlange in July 1975 when the salinity was 3‰.

In this paper a report is given of a fish mortality in the Bot River estuary that occurred during the first week of October 1981, shortly after an artificial breaching of the dune barrier separating the estuary from the sea.

The Bot River estuary (Fig. 1) is situated between 34°19′ to 34°23′S and 19°04′ to 19°09′E on the south-western Cape coast of South Africa. It is normally a closed estuary but has intermittent connections with the sea via two routes: firstly, a deep, artificially opened mouth through the dune barrier near Sonesta and secondly, an overflow channel in the dune slacks which connects with the Kleinmond estuary. These connections, in conjunction with seasonal changes in rainfall and temperature, govern the water-level, temperature and salinity within the estuary. Details of these changes, their effects on the ecology and implications for management of the estuary are

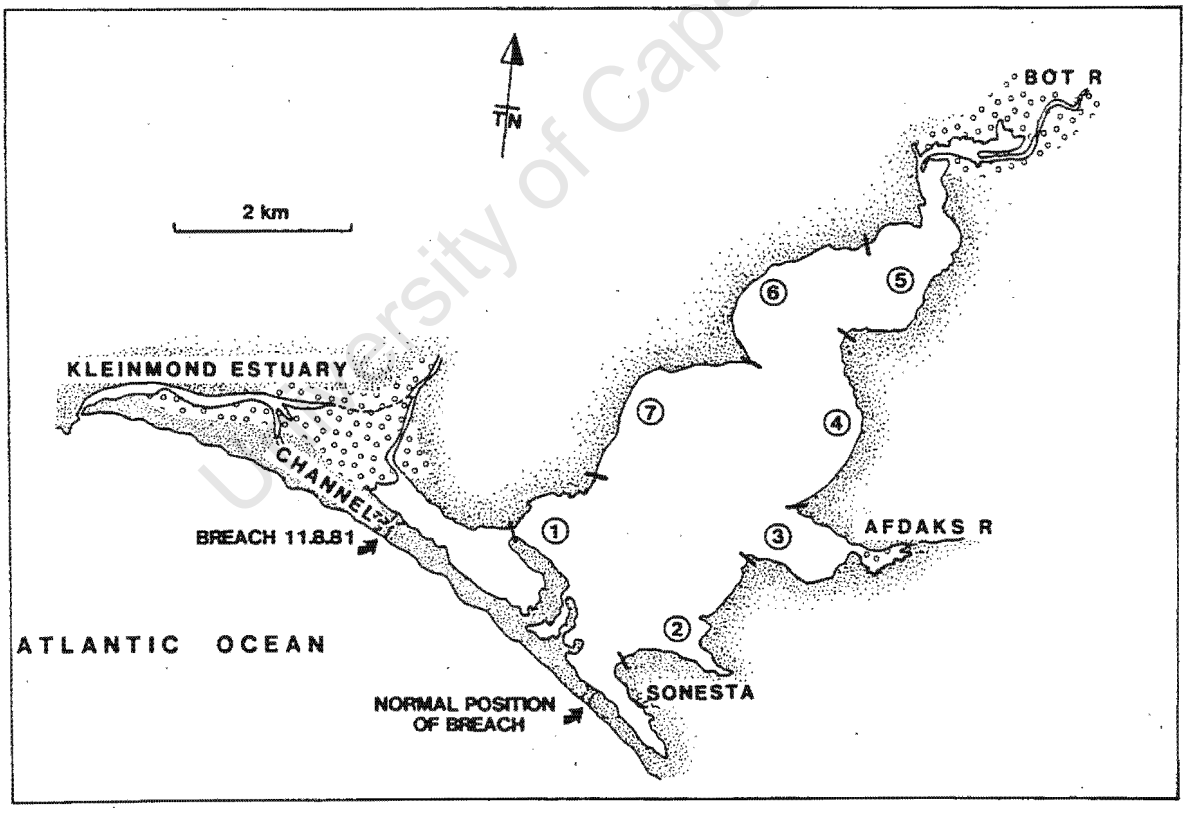

Fig. 1. The Bot River estuary, showing the subdivision of the shoreline into seven areas in which counts of stranded dead fish were made.

provided in Koop (1982), Bally & McQuaid (1985), Bennett *et al.* (1985) and Branch *et al.* (1985).

METHODS

The fish fauna of the estuary was sampled regularly prior to the mass mortality as part of a larger-scale sampling programme (see Bennett *et al.* 1985 for details). Immediately after the mass mortality dead fish were sampled from seven sites around the estuary (Fig. 1), and salinity and temperature measured (with an accuracy of 1‰ and 1 °C), using an American Optics salinometer and a mercury thermometer. Previous measurements of salinity and temperature show that the estuary is well mixed and that measurements at one metre are representative of the water column (Koop 1982, Bally & McQuaid 1985).

The shoreline of the estuary was subdivided into seven areas (Fig. 1), each containing one shore-count. Total numbers of dead fish were then estimated by multiplying the count per 100 m by the length of each section of shoreline. This method of sampling may underestimate species which were selectively removed by scavengers before the counts were made (particularly *Lithognathus lithognathus*) and those species which did not float and become cast ashore but, since almost 20% of the shoreline was sampled, the counts are likely to be representative.

RESULTS

Conditions prior to the mortality

The changes in water-level, temperature and salinity that occurred before and after the fish mortality are shown in Figure 2. Temperatures followed a normal seasonal cycle being highest (about 22,5 °C) in midsummer and lowest (about 12,0 °C) in midwinter. When the estuary is closed water-levels are usually high during the winter rains and low during the dry, hot and windy summer months. In winter when levels rise, a low-lying area between the western arm of the estuary and the adjacent Kleinmond estuary acts as a spillway. It allows water to flow out of the lagoon when the level exceeds approximately 2,25 m but, since its threshold is above the level attained by the highest tides, no salt water can enter. Saline estuarine water is therefore replaced by fresh water from the catchment. Salinities in the estuary fluctuate seasonally due to evaporative concentration and dilution by rains but follow a declining trend because saline water is lost through the Kleinmond overflow. This decline is usually arrested by artificially opening the mouth near Sonesta at two- to four-year intervals, which causes the estuary to become tidal. The estuary soon closes, seldom remaining open for more than a few weeks.

Exceptionally heavy unseasonal rainfall during the summer of 1980–1981 caused continually high water-levels in the estuary and a consequent decrease in salinities (Fig. 2). When the winter rains commenced the water-level was already high and a rapid further increase resulted. These very high water-levels caused some hardship to waterfront landowners and a decision was taken to breach the estuary to reduce water-

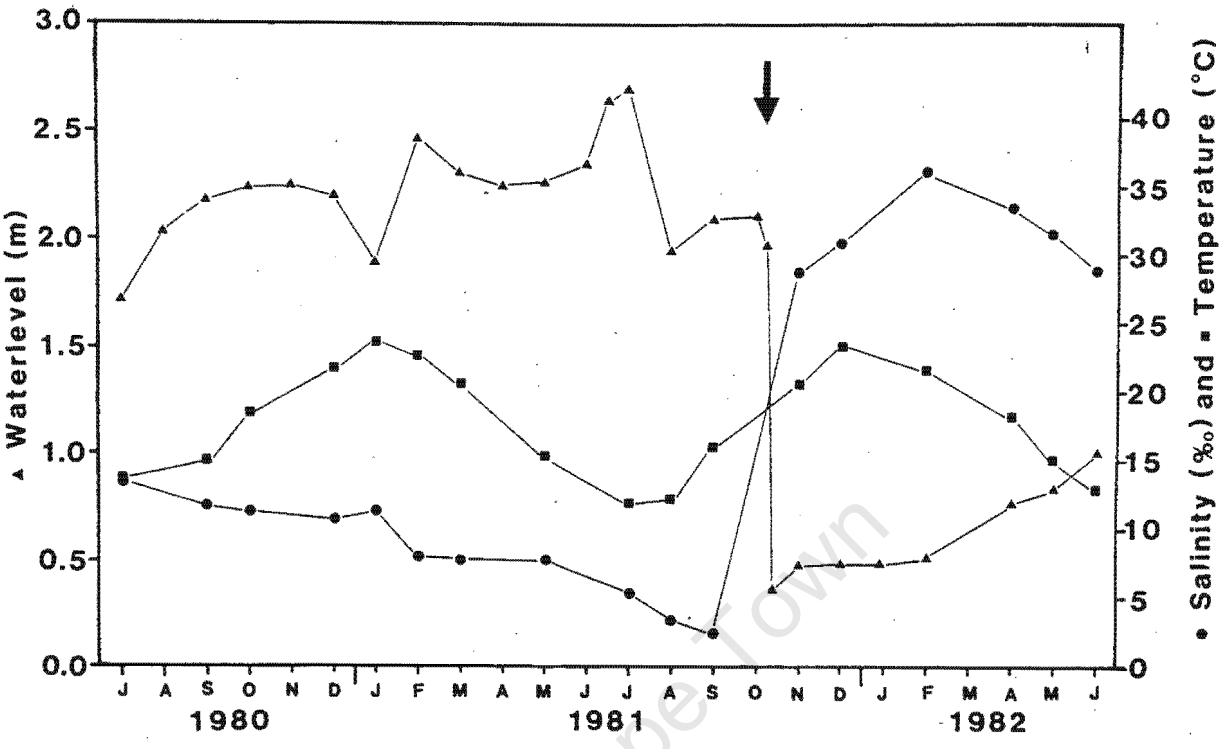

Fig. 2. The water-level and average surface temperatures and salinities in the Bot River estuary between July 1980 and June 1982. Data from Coetzee (1985), Koop (1982) and De Decker (unpubl.). The arrow indicates when the mass mortality occurred.

levels. This breach, on 11 August 1981, was not made at the traditional site near Sonesta but in the western arm of the estuary (Fig. 1), with the object of reducing the normally massive outflow of water and loss of aquatic plants that occur after breachings at Sonesta. The base level in the western arm is 1,7 m above mean sea-level, above the high tide level. This breach therefore operated in a similar way to the Kleinmond overflow but, because its effect was more exaggerated, it reduced the volume of the estuary, and the diluting effect of the fresh-water input was relatively greater than normal, causing a more rapid decline in salinity accompanied by the mass mortality of fish. The estuary was subsequently breached a second time, at Sonesta (Fig. 1), allowing tidal exchange.

Conditions during the mass mortality

Salinity and temperature measurements around the estuary at the time of the mortality are shown in Table 1. Salinities were marginally higher in the southern areas than they were in the head region (3‰ *vs.* 2‰), whereas temperatures were slightly higher in the shallow upper reaches than they were adjacent to deep water nearer the mouth (18 °C *vs.* 16 °C).

The species composition and numbers of dead fish washed up in seven areas around the lagoon are shown in Table 1. A total of 1 616 fish of nine species was counted over 4,2 km (18,5 % of the entire shoreline). When calculated for the entire shore, over 7 000 fish are estimated to have died and become stranded. The species

Table 1
Prevailing temperatures and salinities and the species composition and abundance of fish killed by hyposaline conditions in seven areas around the Bot River estuary. Abundance is expressed as the number of dead fish observed per kilometre of shoreline over which counts were made

	AREA							Calculated
	1	2	3	4	5	6	7	Totals
Salinity (‰)	3	3	3	2	2	2	2	
Temperature (°C)	16	16	16	17	18	18	18	
Distance counted (m)	2 130	300	200	250	200	200	900	4 180
Shoreline (km)	3,2	3,1	2,9	3,3	3,8	3,4	2,9	22,7
SPECIES								
Galeichthys feliceps	339	513	415	368	15	85	250	6 166
Rhabdosargus globiceps	68	10	10	68	5		28	602
Lithognathus lithognathus	20	7	5	8	5		19	199
Ophisurus serpens	16	3		4			16	117
Liza richardsoni						5	3	27
Diplodus sargus	1						1	8
Syngnathus acus							2	6
Pomatomus saltatrix							1	3
Argyrosomus hololepidotus	1							2
Number of fish (km^{-1})	445	533	430	448	25	90	320	
Estimated total (whole area)	1 424	1 653	1 247	1 478	95	306	928	7 130

which died in greatest numbers was *Galeichthys feliceps* (1 616 fish or 86,5% of the total), but large numbers of *Rhabdosargus globiceps* (602), *Lithognathus lithognathus* (199) and *Ophisurus serpens* (177) were also killed. Greatest mortality apparently occurred in the southern areas where up to 533 fish per kilometre were counted. Only 25 fish per kilometre were found near the head of the estuary.

DISCUSSION

Classification of fish according to salinity tolerance

Day (1951) and Whitfield *et al.* (1981) have categorized fish that commonly enter estuaries into four groups according to their origins, reproductive biology and distribution in relation to salinity. Stenohaline marine species are most abundant where salinities approximate those of sea-water, their lower limit being approximately 25‰. Euryhaline marine species can tolerate salinities above 5‰. Typically they enter estuaries as juveniles, many of them being dependent on estuaries during this phase of their life cycles (Wallace *et al.* 1984). They do not, however, spawn in estuaries, possibly because their egg and larval phases cannot tolerate estuarine conditions (Wallace 1975a). True estuarine species breed successfully under estuarine conditions. They are most abundant between 5‰ and 25‰ but can survive a wider range. The final group comprises euryhaline species of fresh-water origin. These usually occur only where salinities are less than 5‰.

Table 2 allows comparison of the numbers and species of fish that were killed with the composition of the fish fauna prior to the mortality and with the categorization of these species according to the classification of Day (1951) and Whitfield *et al.* (1981) outlined above. No species generally categorized as stenohaline marine visitors to estuaries were observed among the dead fish. There is no information on the lower lethal salinity limits of the stenohaline marine species that have been recorded in the Bot River estuary—*Pomadasys olivaceum, Diplodus sargus* and *Trachurus capensis*—but the lowest salinity in which live individuals were sampled from the Bot River estuary was 8,5‰ (Table 2). They were not caught after April 1981 and are therefore considered to have died out at about this time, well in advance of the mass mortality of the remaining species.

In the absence of samples taken after the mortality but before the second artificial opening of the estuary (at Sonesta), no firm conclusions on the proportions of the populations of each species that died can be made. However, judging from catches made prior to the mortality, it is likely that all *Galeichthys feliceps, Rhabdosargus globiceps, Diplodus sargus, Argyrosomus hololepidotus* and *Ophisurus serpens* died, since the number of dead fish greatly exceeded the numbers caught beforehand. A large proportion of the *Lithognathus lithognathus, Pomatomus saltatrix* and *Syngnathus acus* may have been killed whereas most *Liza richardsoni* probably survived. All of these species are considered to be euryhaline marine fish, but they differ in their susceptibility to low salinities. The order in which they succumbed gives an indication of their tolerance and the proportional mortality of each species.

It was evident that the first fish to die had done so at least a week prior to the time

Table 2

The species composition and abundance of fish sampled from the Bot River estuary at intervals prior to the mass mortality, the numbers of fish estimated to have died in October 1981, the minimum salinities in which the species had previously been recorded and their classification as either stenohaline marine (SM), euryhaline marine (EM), true estuarine (TE) or freshwater (FW) species. November 1977 gill-net data are from Ratte (1978), 1980–81 gill and seine-net data from Bennett *et al.* (1985), minimum salinity records from Whitfield *et al.* (1981) and 1980–81 salinities from Coetzee (1985). No seine-net samples were taken in August 1981

	1977	1980			1981		Killed	Min.	
	Nov	Jul	Nov	Feb	Apr	Aug	Oct	Salinity	Class
Gill Nets									
Liza richardsoni	543	103	95	101	109	375	27	1	EM
Galeichthys feliceps	225	65	81	65	77	187	6 166	8	EM
Lithognathus lithognathus	98	114	25	113	159	115	199	1	EM
Mugil cephalus	55	37	1	29	24	14		0	EM
Lichia amia	26	14	12	32	26	18		2	EM
Rhabdosargus globiceps		4	33		1	1	602	3	EM
Caffrogobius multifasciatus			1	4	1	21		—	TE
Rhabdosargus holubi		1	9	5	1	5		1	EM
Pomatomus saltatrix	3	2	2	6	3	1	3	10	EM
Sarpa salpa	2			12				8	EM
Cyprinus carpio				6	3	3		0	FW
Monodactylus falciformis				2	4			0	EM
Liza tricuspidens	1			2				9	EM
Trachurus capensis		1		2				—	SM
Pomadasys olivaceum			2	1				—	SM
Diplodus cervinus		2			1			—	SM
Solea bleekeri				1		1		1	EM
Micropterus salmoides				2				0	FW
Diplodus sargus		1					8	8	SM
Argyrosomus hololepidotus	1						2	1	EM
Liza dumerili	1							1	EM
Seine Nets									
Hepsetia breviceps		467	1 033	1 234	495			0	TE
Gilchristella aestuarius		38	59	196	209			0	TE
Clinus spatulatus		8	133	3	3			—	TE
Psammogobius knysnaensis		8	54	4	33			8	TE
Syngnathus acus		1	2	1	1		6	8	TE
Oreochromis mossambicus		1		1				0	FW
Hyporhamphus knysnaensis				1				1	EM
Not Sampled									
Ophisurus serpens							117	—	EM
Mean Salinity		13.5	11.2	8.0	7.9	3.4	2.4		
Maximum Salinity		14.5	12.0	8.5	8.5	4.5	3.		

that counts were made. During this period the water-level had fallen by approximately 10–15 cm, representing a horizontal distance of 20 m in some places. The level at which the fish were stranded and their state of dehydration or decomposition indicated the order in which the different species had succumbed. The first to die was *G. feliceps* followed by *O. serpens*, *R. globiceps* and *D. sargus*, in that order. *Lithognathus*

lithognathus and *Liza richardsoni* were the last species to die. Other species died either in small numbers or were found on steeply-sloping shores so the relative time of their death could not be estimated. The suggestion that all *G. feliceps, O. serpens* and *R. globiceps* may have died is supported by the fact that all dead individuals of these three species were stranded above the water-line of the day the count was made. The dead *Liza richardsoni* had not yet become stranded by receding water-levels indicating that they had recently died, whereas some live *Lithognathus lithognathus*, showing signs of severe stress, were observed in the shallows. It is therefore probable that not all individuals of these two species had died.

None of the species capable of breeding in estuaries *(Caffrogobuis multifasciatus, Clinus spatulatus, Gilchristella aestaurius, Hepsetia breviceps, Psammogobius knysnaensis* and *Syngnathus acus)* died during the period of low salinity (Table 2). As would the expected, all three fresh-water species *(Cyprinus carpio, Micropterus salmoides* and *Oreochromis mossambicus)* survived and, indeed, tended to occur in the estuary only after flooding diluted salinities (Bennett *et al.* 1985).

Salinity ranges

Whitfield *et al.* (1981) have published a list of salinity ranges for fish common in estuaries along the east and south coasts of South Africa. Twenty-one of the species found in the Bot River estuary are included in this list, and their lower limits are shown in Table 2. From available evidence it appears that a number of them survived lower salinities in the Bot River estuary than previously recorded by Whitfield *et al.* (1981). They are *G. feliceps, P. saltatrix, D. sargus, S. acus* and *Psammogobius knysnaensis*. Whitfield *et al.* give their lower limits as approximately 8‰. The maximum salinity in the lagoon was 8‰ in May 1981 and it declined thereafter (Fig. 2), but none of these species died until the salinities dropped to 2–3‰ in October. These fish therefore had survived for five months in salinities lower than those in which they had previously been recorded. Conversely other species were found dead even though the lagoon was more saline than the lower limits given for these fish. To exemplify, *Argyrosomus hololepidotus, Lithognathus lithognathus* and *Liza richardsoni* have been recorded in salinities of approximately 1‰ but some individuals of these species died in 3‰. Three factors may explain the unexpected deaths of these species, namely, fish-size, water-temperature and the duration of exposure to low salinities. Juveniles may be more tolerant of low salinities than the relatively large individuals which died in the Bot River estuary, all of which were more than three years old. Low temperatures may reduce the osmoregulatory capacity of these species as Blaber (1973) has shown for *Rhabdosargus holubi*. The minimum temperature during the mortality was about 16°C. Although this temperature is not extreme, the fish may have survived had the water been warmer. The maximum salinity had been 3‰ for at least two weeks prior to the mortality, thus the fish had survived for some time in the salinity that proved lethal. If the duration of exposure had been less these species might not have been killed. Evidence that all the species that were killed were avoiding the lowest salinities is provided by the fact that most dead fish were found in the southern areas of the estuary where salinities were highest.

Survival in a fresh-water regime

Not all the species known to be present in the lagoon prior to the mortality were killed. Three of the species which were not killed were from fresh-water and twelve of marine origin. Although some of the surviving marine species can occur in fresh-water it is not known how long they survive under these conditions. Studies in Lake Sibaya and Groenvlei have shown that *Gilchristella aestuarius* and *Hepsetia breviceps* can survive and reproduce under fresh-water conditions (Allanson *et al.* 1974, Ratte & Hanekom 1980). This implies that these are the only marine species that will survive in the Bot River estuary if it becomes a fresh-water lake, which is likely if it is not artificially breached periodically. The Kleinmond overflow will, however, provide an intermittent connection between the lagoon and the sea even when the mouth is closed. Some species, for example *Liza richardsoni, Rhabdosargus holubi* and *Mugil cephalus* do use this overflow as a migration route although only *L. richardsoni* uses it to any great extent (Bennett *et al.* 1985). It is not known whether species such as *Monodactylus falciformis, Myxus capensis* and *Mugil cephalus*, which have been recorded from fresh-water, would use the Kleinmond overflow to enter the Bot River estuary were it to remain permanently closed. It is, however, possible that these migrant species, together with *H. breviceps* and *G. aestuarius*, and possibly some of the other small species which breed in the estuary, would continue to exist in the estuary even under fresh-water conditions.

Implications for management

Fresh-water input from the catchment and the loss of lagoon water via Kleinmond cause salinities in the Bot River estuary to decline throughout the time that it is closed. If closed for long enough, the estuary will eventually contain only fresh-water. Mass fish mortalities can therefore be expected during every period of prolonged isolation from the sea. The mortality described in this report occurred after four years of closure during which time the salinity fell to 3‰.

If the estuary were never opened artificially, it would probably support some of the species that inhabit it under the present regime, but the total number of species would be greatly reduced. Among the species likely to disappear would be *Lithognathus lithognathus, Lichia amia, Rhabdosargus holubi, R. globiceps, Mugil cephalus, Liza richardsoni, Pomatomus saltatrix* and *Argyrosomus hololepidotus*. These are the species which attract fishermen and supply the overwhelming majority of the catch taken in the estuary. The Bot River estuary would, therefore, cease to be the productive fishing area that it now is. In addition the estuary would no longer function as nursery ground for estuarine-dependent species. The Bot River estuary is the third largest estuarine area in the Cape Province and its loss as a nursery area to species such as *L. lithognathus, R. holubi* and *L. amia*, which are entirely dependent on estuaries as juveniles (Wallace *et al.* 1984), would therefore reduce the populations of these important sport-fishing species. For the same reason, *Caffrogobius multifasciatus* and *Psammogobius knysnaensis*, which are dependent on estuaries throughout their life-cycles, may be adversely affected and *Clinus spatulatus*, a species known only from the Bot River estuary (Bennett 1983), may become extinct.

If the Bot River estuary is to continue as a productive fishing area and as a habitat for estuarine-dependent species, salinities must not be allowed to fall to, and remain below, lethal levels. On the basis of information presented in this report, it is suggested that the salinity of the lagoon be regularly monitored and when the maximum falls to 4‰ the dune barrier opposite Sonesta should be artificially breached. It is appreciated that conservation of the marine species is but one facet of the information that must be drawn upon to manage the Bot River estuary. Nevertheless, if the estuary is to be maintained as an estuary—albeit one that is closed for long periods—and not be allowed to progress into a fresh-water lake, artificial breaching is imperative.

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CHAPTER 11.

S. Afr. J. Zool. 1989, 24(3)

The diets of fish in three south-western Cape estuarine systems

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The stomach contents of 2756 fish of 14 species taken by seine and gill netting in the Bot River, Kleinmond and Palmiet estuaries on the south-western Cape coast of South Africa were examined. The small juveniles of all species consumed primarily zooplankton before switching to their adult diets. Seven of the species, *Atherina breviceps, Caffrogobius multifasciatus, Clinus spatulatus, Galeichthys feliceps, Gilchristella aestuaria, Monodactylus falciformis, Psammogobius knysnaensis* and *Syngnathus acus* were carnivores which fed primarily on invertebrates; two, *Hyporhamphus capensis* and *Sarpa salpa*, were herbivores; three, *Lithganathus lithognathus, Rhabdosargus globiceps* and *R. holubi* were omnivores and two, *Lichia amia* and *Pomatomus saltatrix* were piscivores. Within these trophic groupings variations in the diets of fish from the different estuaries were noted as were changes in diet with season. Differences between estuaries were ascribed primarily to food availability and differences in the size ranges of the fish species sampled in them. Differences in the diet between size classes were primarily due to an increasing ability to handle larger food items. The few seasonal differences in diet that occurred appeared not to conform to any observable pattern. Twelve food categories provided > 1% of food consumed by at least one species and each of these categories was represented in the guts of between 9 and 14 of the fish species examined. Six of the prey categories, Isopoda, Amphipoda, Decapoda, Teleostei, Algae and Spermatophyta each provided > 10% of the food consumed by all 14 species combined.

Die maaginhoude van 2756 individue van 14 visspesies wat deur middel van trek- en kiefnette in die Botrivier-, Kleinmond- en Palmiet-estuariums aan die suidwes-Kaapse kus van Suid-Afrika versamel is, is ondersoek. Die klein onvolwassenes van alle spesies het hoofsaaklik soöplankton ingeneem voor oorskakeling na 'n volwasse dieet. Sewe van die spesies, *Atherina breviceps, Caffrogobius multifasciatus, Clinus spatulatus, Galeichthys feliceps, Gilchristella aestuaria, Monodactylus falciformis, Psammogobius knysnaensis* en *Syngnathus acus* was karnivore wat hoofsaaklik ongewerweldes vreet; twee, *Hyporhamphus capensis* en *Sarpa salpa* was herbivore; drie, *Lithognathus lithognathus, Rhabdosargus globiceps* en *R. holubi* was omnivore en twee, *Lichia amia* en *Pomatomus saltatrix* was visvretend. Variasies in die dieet van visse van die onderskeie estuariums, asook die seisoenale dieetverskille, is binne hierdie trofiese klasse aangeteken. Dieetverskille tussen die estuariums word hoofsaaklik toegeskryf aan beskikbaarheid van voedsel en aan die verskille in grootteklasse van die versamelde vissoorte. Dieetverskille tussen vis-grootteklasse was hoofsaaklik 'n gevolg van 'n toenemende vermoë om groter voedselitems te hanteer. Die enkele seisoenale dieetverskille kon aan geen ooglopende patroon gekoppel word nie. Twaalf voedselklasse het meer as 1% van die voedselinname van ten minste een spesie uitgemaak, en elkeen van hierdie klasse is in die maaginhoud van tussen 9 en 14 vissoorte verteenwoordig. Ses van die prooiklasse, Isopoda, Amphipoda, Decapoda, Teleostei, Algae en Spermatophyta het elk meer as 10% van die gesamentlike voedselinname van al 14 spesies uitgemaak.

A considerable amount of information concerning the diets of fish in South African estuaries is available. Published studies include descriptions of the diets of individual species (e.g. Blaber 1974, 1984; Whitfield & Blaber 1978a; Coetzee 1981, 1982a; Coetzee & Pool 1985), taxonomic groups (Masson & Marais 1975; Blaber 1976; Cyrus & Blaber 1983) and guilds (Whitfield & Blaber 1978b; Blaber 1979; Marais 1984). Also included are descriptions of the morphological and ecological inter-relationships between the fish and their food resources (Whitfield 1980; Blaber, Cyrus & Whitfield 1981; Cyrus & Blaber 1982; White & Bruton 1983; Whitfield 1984). All the work mentioned above was conducted on fish in estuaries on the eastern, south-eastern and southern coasts of South Africa and, with the exception of the data provided on *Rhabdosargus globiceps* in the Hermanus lagoon (Talbot 1955), there is no published information on the diets of fish in south-western Cape estuaries.

The data presented in this paper were obtained from fish sampled in three south-western Cape estuaries, namely the Palmiet, Kleinmond and Bot River estuaries (Figure 1). General information on the physical and biological characteristics of these estuaries are provided by Koop (1982); Koop, Bally & McQuaid (1983) and Branch & Day (1984). The main difference between these estuaries is that the Palmiet is usually permanently open to the sea, the Kleinmond is open periodically each year and the Bot River estuary is usually only in contact with the sea for brief periods every 2–4 years after artificial opening. Details of many aspects of the biology and life histories of the fishes inhabiting these estuaries are provided by Bennett (1985, 1989) and Bennett, Hamman, Branch & Thorne (1985).

Methods

Fish were obtained from the Palmiet, Kleinmond and Bot River estuaries with seine and gill nets as described by Bennett *et al.* (1985) and Bennett (1989). Following capture, subsamples were preserved in 10% formalin for analysis of stomach contents. For this purpose fish were either preserved whole if small (< ± 50 mm), or after

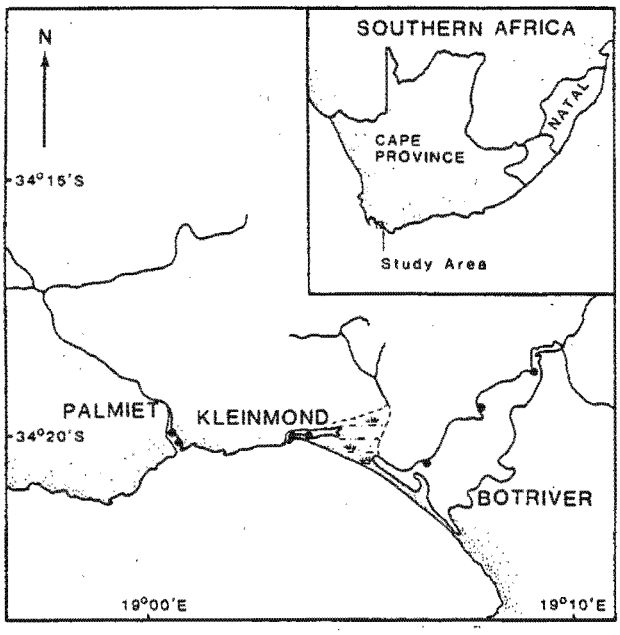

Figure 1 A map of southern Africa showing the locations of the Bot River, Kleinmond and Palmiet estuaries which were sampled to obtain fish specimens for stomach content analysis.

having a midventral abdominal incision made (fish of 50–150 mm), or, in the case of larger fish (> ± 150 mm), stomachs were removed and preserved separately. Stomachs were selected to represent the full size range of each species in each estuary throughout the year.

In the laboratory each stomach was emptied separately into a glass container under a dissecting microscope where the food items that it contained were identified to the lowest possible taxon. The amount of each prey species was measured as the volume displaced in a measuring cylinder, unless the volumes were small (< ± 0,1 cm^3), when estimates were made by flattening the prey items to a thickness of 1 mm using microscope slides and then counting the number of 1-mm squares of a grid placed under the container that were obscured.

Data on stomach contents were recorded separately for each fish together with the species, total length (mm), locality and date of capture of that specimen. Summaries of the percentage volume (%V) and frequency of occurrence (%O) (Hynes 1950; Berg 1979) of each prey species (or of the prey species grouped into higher taxa), were prepared to show differences in diet between each fish species, between the different size classes of each species, for each species in the three different estuaries and at different times of the year.

Results and Discussion

Seventeen species of fish are listed by Bennett (1989) as being either abundant or common in south-western Cape estuaries. Of the 14 species examined in this study, 12 appear on this list and provided > 99% of fish sampled in the Palmiet, Kleinmond and Bot River estuaries. Two rare species (*S. salpa* and *H. capensis*) were included because they are the only species which were primarily herbivorous. The five common or abundant species not included were *Liza richardsoni, Mugil cephalus, Myxus*

Table 1 The total number of fish examined for stomach contents from three south-western Cape estuaries sampled in 1980 and 1981. For each estuary the species composition and size range of fish sampled and the number of stomachs that contained food are shown

	Total No. of guts	Palmiet		Kleinmond		Bot River		Total No. with food
		No.	Size	No.	Size	No.	Size	
Atherina breviceps	768	76	28–75	144	23–96	273	21–97	493
Caffrogobius multifasciatus	136	88	31–165			28	28–148	116
Clinus spatulatus	50					47	23–132	47
Galeichthys feliceps	129	11	120–295			102	170–402	113
Gilchristella aestuaria	94	25	43–78			63	22–61	88
Hyporhamphus capensis	6					6	110–182	6
Lichia amia	73	3	71–460	12	95–495	39	443–820	54
Lithognathus lithognathus	346	72	20–294	100	22–268	138	252–660	310
Pomatomus saltatrix	53	5	43–125	5	82–122	31	453–632	41
Psammogobius knysnaensis	871	191	22–60	222	18–69	191	21–61	604
Rhabdosargus globiceps	78	19	28–192	26	27–134	22	208–340	67
R. holubi	65	14	20–195	33	22–155	12	271–368	59
Sarpa salpa	6					6	257–275	6
Syngnathus acus	81					77	41–158	77
Totals	2773	504		542		1035		2081

Table 2 The diets of fourteen fish species from the Bot River, Kleinmond and Palmiet estuaries in the south-western Cape. Only prey categories that contributed >0,5%V consumed by at least one species are included (– indicates < 0,5% contribution to occurrence or volume)

	Food category																							
	Polychaeta		Copepoda		Ostracoda		Isopoda		Amphipoda		Tanaidacea		Decapoda		Insecta		Mollusca		Teleostei		Algae		Spermato-phyta	
Species	%O	%V	%O	%V	%O	%V	%O	%V	%O	%V	%O	%V	%O	%V	%O	%V	%O	%V	%O	%V	%O	%V	%O	%V
Atherina breviceps	3	1	39	6	31	11	8	10	43	35	2	–	7	3	32	26	6	2	6	2	3	1	1	–
Caffrogobius multifasciatus	34	3	9	–	3	–	43	12	97	20	55	3	12	34	27	2			10	20				
Clinus spatulatus	4	–	21	–	19	1	64	37	94	32					51	4	13	23	4	2	2	–	6	–
Galeichthys feliceps	4	–			1	–	58	6	37	9			83	79	15	4	8	–	13	2				
Gilchristella aestuaria	1	1	67	22	60	33	3	–	33	10	7	3			31	12	16	5	14	5	8	2	1	–
Hyporhamphus capensis			17	–	17	–							17	–	100	5			50	1			50	93
Lichia amia													6	–					100	100				
Lithognathus lithognathus	20	–	14	–	14	–	45	5	55	9	14	–	19	21	54	1	36	23	4	1	46	29	16	9
Pomatomus saltatrix						5	–						10	–					100	100				
Psammogobius knysnaensis	26	11	25	2	27	6	10	4	66	47	6	1	3	2	45	22	3	–	3	2	2	–	–	
Rhabdosargus globiceps	18	–	16	–	27	–	60	–	66	–	16	–	58	20	30	–	76	23	7	8	47	46	21	2
R. holubi			22	–			36	–	71	1	10	–	54	18	61	1	54	20			73	29	37	31
Sarpa salpa															50	1	17	–			100	53	83	46
Syngnathus acus			81	43	8	–	22	13	44	42	1	–			19	2	6	–						

capensis, *Liza dumerilii* and *Oreochromis mossambicus*. Preliminary examinations of the stomach contents of these five species revealed diets similar to those recorded in the literature i.e. fry of $< \pm 30$ mm consumed zooplankton and larger fish contained a mixture of sediment, detritus and benthic diatoms (Blaber 1976, 1977; Blaber & Whitfield 1977; Masson & Marais 1975; Whitfield 1980; Whitfield & Blaber 1978c). The decision not to include detailed analyses of the diets of these species was taken partly because of practical difficulties in the identification, separation and quantification of their stomach contents but more particularly because the published information adequately reflects their diets in the south-western Cape.

A total of 2756 stomachs from 14 species of fish were examined during the course of this study, 2081 of which contained food, 504 of them from 10 species captured in the Palmiet estuary, 542 from seven species from the Kleinmond estuary and 1035 in 14 species in the Bot River estuary (Table 1). The percentage occurrence and composition of each of the 12 major prey categories found in the guts of each species from all three estuaries combined are presented in Table 2. From this table it is apparent that the majority of species consume a wide variety of prey but that in all cases only one or two categories provide the bulk of the diet. Of the 14 species investigated, seven (*Atherina breviceps, Psammogobius knysnaensis, Gilchristella aestuaria* and *Caffrogobius multifasciatus* being most abundant) fed primarily on small invertebrates, two (*Hyporhamphus capensis* and *Sarpa salpa*) were herbivorous; two (*Lichia amia* and *Pomatomus saltatrix*) were piscivorous and three (*Lithognathus lithognathus, Rhabdosargus globiceps* and *R. holubi*) were omnivorous (Table 3). Despite the generality of these trophic groupings the food items consumed often differed quite markedly between fish species within a particular group, and between the same fish species in the three different estuaries (Table 4). Intraspecific differences in diet were also observed, both seasonally and between different size classes, as outlined for each of the following species.

Atherina breviceps

A total of 768 *A. breviceps* stomachs was examined of which 275 were empty or nearly so. Of the 493 stomachs included in this analysis 76 were of fish from the Palmiet, 144 from the Kleinmond and 273 from the Bot River estuaries. The stomachs containing food all came from fish of between 21 and 97 mm in length (Table 1).

Invertebrates provided the bulk of the diet of this species in the three estuaries with amphipods (43%O, 35%V), insects (32%O, 26%V — primarily aquatic chironomid and odonatan larvae), ostracods (31%O, 11%V) and isopods (8%O, 10%V) being the most important prey categories (Table 4). The prey species contributing the greatest amount to the diet were the amphipods *Corophium triaenonyx, Grandidierella bonnieroides* and *Melita zeylanica* (Table 4).

Differences in the composition of the diet of fish taken from the three estuaries were evident (Table 2).

Table 3 The relative importance of invertebrates, weed and fish in the diets of fish from the Bot River, Kleinmond and Palmiet estuaries in the south-western Cape

	Invertebrates		Fish		Weed	
	%O	%V	%O	%V	%O	%V
Carnivores						
Syngnathus acus	100,0	99,8	–	–	–	–
Galeichthys feliceps	100,0	98,0	13,3	2,1	–	–
Clinus spatulatus	100,0	97,0	4,3	2,1	8,5	0,5
Atherina breviceps	99,8	95,9	6,5	1,6	4,3	0,8
Psammogobius knysnaensis	100,0	94,2	3,5	2,0	2,3	0,3
Gilchristella aestuaria	100,0	85,3	13,6	5,3	11,4	2,4
Caffrogobius multifasciatus	100,0	74,9	10,3	19,7	–	–
Piscivores						
Pomatomus saltatrix	14,6	–	100,0	100,0	–	–
Lichia amia	5,6	0,1	100,0	99,9	–	–
Herbivores						
Sarpa salpa	66,7	0,8	–	–	100,0	99,2
Hyporhamphus capensis	100,0	6,2	5,0	0,6	50,0	93,2
Omnivores						
Lithognathus lithognathus	99,7	59,3	3,9	0,5	53,2	38,0
Rhabdosargus globiceps	100,0	44,8	7,5	7,5	77,6	47,6
R. holubi	100,0	40,9	–	–	88,1	59,1

Copepods provided 19% of the total volume consumed by fish in the Palmiet but only 4% and 2% of samples taken in the Kleinmond and Bot River estuaries. Ostracods were, on the other hand, more important in the diets of *A. breviceps* from the Kleinmond (22%V) than either the Palmiet (9%V) or Bot River (5%V) estuaries. Similarly, isopods provided 17% of the volume consumed in the Bot River estuary but less than 3% in the other two estuaries, amphipods provided more than 45% in Palmiet and Bot River estuaries but only 10% in the Kleinmond estuary, and insect larvae provided 46% in the Kleinmond but only 12% and 3% in the Bot River and Palmiet estuaries respectively.

The composition of the diets of three size classes of fish from one locality in the Bot River estuary is shown in Table 5 and indicates that the diet of *A. breviceps* changes with size. Small individuals (< 25 mm) consumed primarily copepods (56%V) and molluscan larvae (18%V) whereas fish of intermediate size (25–50 mm) fed largely on amphipods (47%V) and insect larvae (12%). Larger fish (> 50 mm)consumed a wider variety of prey with amphipods (24%V), isopods (17%V), gastropods (10%V) and decapods (10%V) all being important. These changes, which primarily involved a decrease in the proportion of small planktonic organisms

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Table 4 The composition (%V) of the diets of 14 fish species from the Bot River (B), Kleinmond (K) and Palmiet (P) estuaries. Only prey species that constituted > 5%V in at least one species from at least one estuary are included (– indicates < 0,5%V)

	Atherina breviceps			*Caffrogobius multifasciatus*		*Clinus spatulatus*			*Caleichthys feliceps*			*Cilchristella aestuaria*			*Hyporhamphus capensis*	*Liza richardsoni*			*Mugil cephalus*			*Pomatomus saltatrix*			*Psammogobius knysnaensis*			*Rhabdosargus globiceps*			*R. holubi*			*Sarpa salpa*	*Syngnathus acus*
	B	K	P	B	P	B	B	P	B	P		B	K	P		B	K	P	B	K	P	B	K	P	B	K	P	B	K	P	B	K	P	B	B
Polychaeta																																			
Ceratonereis erythraeensis		–	1	3													–	2	–							3	6	3							
Crustacea																																			
Copepoda																																			
Pseudodiaptomus hessi	1	–	2			–			4								15	–								1	1	–						27	
Calanoidea	–	2	12						9	20																								8	
Ostracoda	5	22	9			1	–		30	43	–					–	–									7	5	7		1	1		2	3	–
Isopoda																																			
Cyathura estuaria	–		1	8	5	1	3	–								2		–		4					–	–	4	–		2		1	1		
Exosphaeroma hylecoetes	1	3	15	4	–	30	3									4	1								2	–	–							8	
Amphipoda																																			
Corophium triaenonyx	22		–	9	–	4			4							–	–	–							14	–	–		–		–	–		14	
Grandidierella bonnieroides	5	7	30	–	20			63	1	3							2	7							2	14	73		–	3	–	1	2		
Melita zeylanica	17	1	9	8		28	4		7							8	68								15	12	–	–	2	1	–	1	1	27	
Talorchestia sp.		–	6																																
Decapoda																																			
Callianassa kraussi	–		3	6	6		83	6								7		6		4					4		–	17	18	19	17	10	20		
Cleistosoma edwardsii					1		–																				–		9	5			–		
Hymenosoma orbiculare	4	–	5	12	29						–							61							–		–	1	5	11	2	5	4		
Palaemon pacificus														1			–			10						–									
Insecta																																			
Aquatic larvae																																			
Chironomidae	9	22	2	14	–	3	4	2	14	2						1	1	–							34	35	1	–	1	1	–	2	1	11	
Odonata	2	23									3						4									–									
Adults																																			
Diptera	2	9	3			–			–		–							–							–	–	–								
Mollusca																																			
Gastropoda																																			
Hydrobia sp.	4		–			2	–		4							1		–			–				–		–	23	22	11	19	20	22	–	–
Tomichia sp.						21										–									–			–			1				
Pelecypoda																																			
Arcuatula sp.							–									20												1			–				
Teleostei																																			
Whole fish																																			
Atherina breviceps				16		2	–				–	5	6			–			20	13	7							8							
Caffrogobius multifasciatus					4							5	8			–			2																
Clinus spatulatus				6			–					59				–			16																
Liza richardsoni												26	60				–		4																
Mugil cephalus													22																						
Mugilidae																				31	36														
Pomadasys olivaceum												5							8																
Psammogobius knysnaensis					11								1																						
Rhabdosargus holubi																			5																
Sarpa salpa																			12																
Syngnathus acus																–			14																
Eggs																																			
Psammogobius knysnaensis																									–	5									
Algae																																			
Cladophora sp.							–									24	–	1							–	–	–	47	38	20	26	32	18	38	
Enteromorpha sp.																7	1	22							–	–				15	–	8	20	10	
Spermatophyta																																			
Potamogeton sp.											93					–												–			23	9			
Ruppia sp.	1						–			1						8									–			1			9	6		46	

Table 5 The diets (%V) of three different size classes of *Atherina breviceps* sampled at one locality in the Bot River estuary. Only prey categories which provided more than 5% V in at least one of the size classes are included

Prey category	Size class		
	< 25 mm	25–50 mm	> 50 mm
Copepoda	56	6	1
Ostracoda	–	5	2
Isopoda	–	6	17
Annphipoda	7	47	24
Decapoda	–	–	10
Insect larvae	3	12	9
Adult insects	–	2	5
Gastropoda	–	–	10
Molluscan larvae	18	–	–

and an increase in larger benthic and weed-dwelling forms with increasing fish size, were apparent in all three estuaries.

Sufficient numbers of guts were examined on a monthly basis in the Bot River and Kleinmond estuaries to investigate seasonal changes in diet (Table 6). The majority of the important prey groups occurred throughout the year. Although these quantities varied, there were no strong seasonal patterns. Only *G. bonnieroides* in the Bot River and odonatan larvae in the Kleinmond estuary showed any seasonal pattern, both occurring almost exclusively during the late autumn and winter months.

Previous references to the diet of *A. breviceps* have been made by Blaber (1979), Day, Blaber & Wallace (1981) and Coetzee (1982b). Blaber (1979) examined the guts of 30 fish from lake St Lucia and found that 99% of their calorific consumption was accounted for by the copepod *Pseudodiaptomus stuhlmanni* which was taken by filter feeding. Day *et al.* (1981) stated that *A. breviceps* is a zooplankton feeder but provided no details of the diet. Coetzee (1982b) provided considerably more information from his analysis of stomach contents from fish caught in Groenvlei and Swartvlei. He identified amphipods, isopods and ostracods as the most important food categories but pointed out differences in diet between his two sampling localities which he ascribed to food availability. He also described a change in diet from filter feeding amongst small fish to the active capture of selected organisms by larger fish. In all these respects his observations are similar to the present results obtained for this species.

Caffrogobius multifasciatus

A total of 136 stomachs from this species were examined

Table 6 The monthly contribution (% V) of important prey species in the diet of *Atherina breviceps* in the Bot River and Kleinmond estuaries. Species represented are those which contributed > 5% to overall volume

Prey species	Month											
	J	F	M	A	M	J	J	A	S	O	N	D
Bot River												
Corophium triaenonyx	63	–	62	19	3	–	9	26	3	10	16	7
Exosphaeroma hylecoetes	6	16	–	–	5	31	11	8	–	13	49	15
Melita zeylanica	8	3	18	39	27	–	4	12	1	–	–	9
Grandidierella bonnieroides	–	–	–	11	16	5	6	8	–	–	–	–
Ostracoda	3	12	6	–	–	26	–	4	10	13	–	–
Chironomid larvae	6	–	–	10	4	3	2	6	15	9	8	5
Kleinmond												
Ostracoda	75	1	10	2	2	3	4	2	24	52	1	–
Chironomid larvae	7	17	34	36	–	1	23	4	54	1	3	5
Grandidierella bonnieroides	–	5	–	–	6	–	16	–	–	–	12	17
Odonatan larvae	–	–	–	–	70	5	14	–	–	–	–	–
Dipteran adults	–	4	–	–	11	3	–	–	5	35	9	15

of which 116 (85%) contained food, 88 from fish taken in the Palmiet estuary and 28 from the Bot River estuary (Table 1). This species was not common in the Kleinmond estuary and guts from the few individuals taken there were not examined.

Four categories of prey each provided more than 10% of the total volume consumed by the sample, namely decapods (34%), amphipods (20%), fish (20%) and isopods (12%). Two of these categories occurred in a large proportion of the guts examined (amphipods 97%, isopods 43%), whereas decapods (12%) and fish (10%) occurred less frequently (Table 2).

Some differences in the composition of the diet were evident between samples from the Bot River and Palmiet estuaries (Table 4). In the Bot River estuary *C. triaenonyx* and *M. zeylanica* provided most of the amphipod category whereas in the Palmiet *G. bonnieroides* was the most important species. Chironomid larvae provided 14%V in the Bot River estuary but < 0,5%V in the Palmiet, and the decapod *H. orbiculare* provided 29%V in the Palmiet but less than half that (12%) in the Bot River estuary. The main fish species consumed also differed between the two estuaries. In the Bot River *A. breviceps* was an important source of food (16%V) while in the Palmiet estuary *P. knysnaensis* was more significant (11%V).

Sufficiently large samples were obtained from the Palmiet estuary to examine whether there were any changes in diet with fish size (Table 7). Copepods were found only in fish < 40 mm and tanaids and insect larvae decreased in importance with increasing fish size. Decapods and fish were most important in the diet of the larger fish (> 100 mm) but absent from those < 40 mm.

Clinus spatulatus

Fifty guts of this species were examined of which 47 contained food (Table 1). The sample was obtained entirely from the Bot River estuary as this species is very rare in the Kleinmond and absent from the Palmiet.

All guts contained small invertebrates which provided 97% of the volume of food consumed (Table 3). Isopods (64%O, 37%V), amphipods (94%O, 32%V) and gastropod molluscs (13%O, 23%V) were the most important prey categories (Table 2) and *Exosphaeroma hylecoetes* (30%V), *M. zeylanica* (28%V) and *Tomichia* sp. (21%V) were the most important species (Table 4).

Ostracods and insect larvae provided 29% and 21 % of the total volume consumed by fish of < 30 mm and less than 3% in the larger size classes (Table 8). Amphipods were important throughout the size range sampled, providing approximately 30% of the total volume of food consumed. Isopods and gastropods were more important in the diets of fish of more than 30 mm in length and small fish were consumed only by *C. spatulatus* of over 100 mm in length.

A less detailed report on the diet of this species is provided by Bennett (1983).

Galeichthys feliceps

The stomachs of 129 *G. feliceps* were examined. Of these 113, contained food: 11 from the Palmiet estuary and 102 from the Bot River estuary (Table 1).

Invertebrates provided 98% of the total volume of food consumed by this species with decapods (79%V) the most important prey category and *Callianassa kraussi* (78%V) the most important prey species. This description of the diet is heavily influenced by the large sample obtained from the Bot River estuary. In the Palmiet estuary where fewer, smaller, fish were collected, amphipods, especially *G. bonneroides* (63%V), were most important with decapods (19%V), fish (10%V) and isopods (6%V) all contributing significantly (Tables 2 and 4).

Stomach contents of *G. feliceps* from five other estuaries in the eastern and south-eastern Cape have been reported by Marais (1984) and Coetzee & Pool (1985). There are minor differences in diet between these estuaries but decapod crustaceans (usually *Upogebia africana* and *H. orbiculare*) were the most important food in almost all samples.

Gilchristella aestuaria

Eighty-eight of the 94 stomachs examined contained food and these were from fish of between 22 and 78 mm in length. Most of the fish with food in their stomachs

Table 7 The percentage composition (%V) of the major prey categories in the diet of three different size classes of *Caffrogobius multifasciatus* in the Palmiet estuary

	Size class		
Prey category	< 40 mm	40–100 mm	> 100 mm
Polychaeta	2	1	2
Copepoda	6	–	–
Isopoda	17	13	10
Amphipoda	31	33	13
Tanaidacea	15	9	–
Decapoda	–	28	43
Insect larvae	29	1	–
Teleostei	–	10	24

Table 8 The percentage composition (%V) of the major prey categories in the diets of three size classes of *Clinus spatulatus* from the Bot River estuary

	Size class		
Prey category	< 30 mm	30–100 mm	< 100 mm
Ostracoda	29	–	–
Isopoda	10	31	44
Amphipoda	32	35	29
Mollusca	3	29	18
Insect larvae	21	3	3
Teleostei	–	–	4

were from the Bot River estuary (63), the remainder coming from the Palmiet (Table 1).

Ostracods (60%O, 330%V), copepods (67%O, 22%V), insects (31%O, 12%V) and amphipods (33%O, 10%V) were the most important prey categories (Table 2). A large proportion of the prey consumed by *G. aestuaria* was of larval or juvenile stages from the aforementioned groups which, because of their small size and the degree of digestion, could not be identified to species. Adults of larger prey species that were identified included *Pseudodiaptomous hessi* (3,3%V), *C. triaenonyx* (2,9%V), *M. zeylanica* (5,1%V) and *Hydrobia* sp. (3,1%V). Also of some importance was detritus (3,9%V) (Table 4).

The diet of fish from the Palmiet contained 13% more ostracods and 24% more copepods than fish from the Bot River estuary. This difference was compensated for by the inclusion of more chironomid larvae, amphipods, tanaids and gastropods in the diets of Bot River fish (Table 4).

The diets of small (< 30 mm), intermediate (30–50 mm) and large (> 50 mm) *G. aestuaria* from the Bot River estuary are shown in Table 9. In the small size class copepods (38,7%V), diatoms (17%V) and detritus (11,7%V) provided a substantial proportion of the total amount of food consumed but their importance decreased markedly in fish > 30 mm in length. Ostracods (44,1%V) were the dominant food category in fish of intermediate size although three other categories, amphipods, copepods and insect larvae all contributed between 12 and 14% to the volume consumed. The largest fish (> 50 mm) had more diverse diets. Insect larvae were the main contributors by volume (19,9%) but larger organisms such as polychaetes, gastropods and fish larvae, which were not found in smaller fish, constituted almost a quarter of their diet. Small *G. aestuaria* rely primarily on small invertebrates which they may obtain by filter feeding, whereas larger individuals consume a higher proportion of benthic organisms , suggesting an increasing reliance on prey that are probably selected individually.

Table 9 The percentage composition (%V) of the major prey categories in the diets of three size classes of *Gilchristella aestuaria* in the Bot River estuary

Prey category	Size class		
	< 30 mm	30–50 mm	> 50 mm
Polychaeta	–	–	3
Ostracoda	7	44	18
Copepoda	39	12	14
Tanaidacea	–	4	4
Insect larvae	6	12	20
Gastropoda	2	2	12
Fish eggs	–	2	4
Fish larvae	–	–	7
Diatoms	17	1	–
Detritus	12	4	3

Analyses of the stomach contents of *G. aestuaria* from nine different estuarine, coastal lake and freshwater localities have been reported (Blaber 1979, Blaber *et al.* 1981; Coetzee 1982b; Talbot 1982; White & Bruton 1983). Considerable differences in the major prey categories between localities are evident. In St Lucia, for example, 68% of the calorific contribution to their diet was the copepod *Pseudodiaptomus stuhlmanni* (Blaber 1979), in Lake Nlange chironomid larvae contributed 47% and *P. stuhlmanni* 26% and in the adjacent Lake Makhawulani macruran zoae contributed 87% (Blaber *et al.* 1981). In Swartvlei copepod nauplii and detritus were the major stomach contents and in Groenvlei *Grandidierella lignorum* was most important (Coetzee 1982). Diatoms were found to be the most important food category in the Bloukrans River (White & Bruton 1983). These results show that *G. aestuaria* are capable of consuming a wide variety of food organisms which they obtain either by filtering or by selecting individual larger prey. The relative importance of these two modes of feeding probably varies according to the size spectrum and abundance of available food.

Hyporhamphus capensis

The stomachs of six *H. capensis* (110–182 mm) from the Bot River estuary were examined, all of which contained food. The aquatic macrophyte *Potamogeton pectinatus* provided the bulk of the gut contents (93%V) but it occurred in only half the fish examined. Insects, both aquatic larvae and terrestrial adults, occurred in all stomachs but provided only 5%V (Table 2).

Coetzee (1981) provided a detailed description of the gut contents of *H. capensis* from Rondevlei in the southern Cape. He showed that their diet varied with size, animal material forming the bulk of the gut contents in small (< 9 cm) and large (> 17 cm) fish, with plant material being most important in the intermediate size class. He also showed that the diet of the intermediate sized fish varied seasonally, with plant material being most important in the summer and least important during the spring months.

Lichia amia

The stomachs of 73 *L. amia* were examined and 54 found to contain food. Most of the sample was obtained from the Bot River estuary (39 fish) with only 12 and three from the Kleinmond and Palmiet estuaries respectively. The fish from the latter two estuaries were also considerably smaller (71–495 mm) than those from the Bot River estuary (443–820 mm).

More than 99% of the food consumed by *L. amia* was fish, the only other prey species being the decapod *Palaemon pacificus* which occurred in the stomachs of two small individuals (95–135 mm) from Kleinmond. *A. breviceps* and *C. multifasciatus* occurred in the diets from all three estuaries but provided < 10%V in each case. *Liza richardsoni* was the most important species in the Palmiet (53%V) and Kleinmond (60%V) estuaries whereas *C. spatulatus*, a species rare or absent in these

estuaries, was most important (59%V) in the Bot River estuary.

The stomach contents of *L. amia* have previously been described by Whitfield & Blaber (1978b), Coetzee (1982a), Smale & Kok (1983) and Marais (1984). In all cases the main prey types were similar to those reported above, crustacea and fish being of importance in smaller specimens (< ± 200 mm) whereas larger fish are almost exclusively piscivorous.

Lithognathus lithognathus

Three hundred and forty-six *L. lithognathus* stomachs were examined and 310 were found to contain food; 72 from the Palmiet estuary, 100 from the Kleinmond and 138 from the Bot River estuary. There was only partial overlap in the size of fish sampled from the estuaries. In the Palmiet and Kleinmond estuaries the size range was 20–294 mm and in the Bot River estuary it was 252–660 mm (Table 1).

Table 3 shows that when the data from the three estuaries are combined approximately 60%V of the diet of *L. lithognathus* was invertebrates and 40%V was aquatic plants, so that this species may be considered omnivorous. In the Palmiet estuary the main items consumed were decapods (67%V) and algae (24%V); *H. obiculare*, (61%V) and *Enteromorpha* sp. (22%V) contributing substantially to these respective categories. The diet of this species from the Kleinmond estuary was quite different, amphipods providing the bulk of the diet (69%V) with one species, *M. zeylanica* contributing 68%V. Also important were copepods, almost entirely represented by *P. hessi* (15%V). In the Bot River estuary *L. lithognathus* consumed a wider variety of food. Algae (32%V) were the major category but molluscs (25%V), decapods (21%V), amphipods (9%V) and spermatophytes (9%V) were also important.

The diet of *L. lithognathus* in the Palmiet and Kleinmond estuaries changed as the fish increased in size but the important food categories differed in the two estuaries (Table 10). In the Kleinmond estuary copepods (56%V) and ostracods (38%V) were the most important prey items in fish of less than 30 mm whereas amphipods (46%V) and copepods (34%V) were important in the intermediate class (30–100 mm), and the larger class (> 100 mm) consumed primarily amphipods (76%V). Polychaetes and insect larvae provided between 5 and 11%V in the larger two size classes. In the Palmiet estuary copepods were consumed only by small fish and the proportion of amphipods decreased with increasing fish size from 86%V to 6%V. Decapods and algae, on the other hand, were absent from the stomachs of the smallest size class but of major importance in the largest class where they provided 68%V and 24%V respectively. In the Bot River estuary where no small fish were sampled plant material provided 41%V and a bivalve species 28%V.

Table 10 The percentage composition (%V) of the major prey categories in the diets of three size classes of *Lithognathus lithognathus* in the Kleinmond and Palmiet estuaries

	Size class		
Prey category	< 30 mm	30–100 mm	> 100 mm
Kleinmond			
Polychaeta	–	11	6
Copepoda	56	34	10
Ostracoda	38	1	–
Amphipoda	3	46	76
Insecta	–	6	5
Palmiet			
Copepoda	5	–	–
Amphipoda	86	79	6
Decapoda	–	7	68
Algae	–	1	24

Mehl (1973) found that in the Heuningnes estuary *L. lithognathus* had a varied diet, the composition of which was fairly constant throughout the year. The most commonly consumed prey items were decapods, amphipods, aquatic plants, gastropods and polychaetes. Whitfield (1985) reported that *L. lithognathus* of < 30 mm in Swartvlei consumed primarily amphipods and copepods. Marine samples examined by Lasiak (1984) contained mainly the swimming prawn *Macropetasma africana*, bivalves (*Donax* spp.) and polychaetes.

Pomatomus saltatrix

The stomachs of 53 *P. saltatrix* were examined, 41 of which contained food, five each from the Palmiet and Kleinmond estuaries, where the size range was 43–225 mm, and 31 of between 435 and 623 mm from the Bot River estuary (Table 1).

This species was almost exclusively piscivorous. All guts contained fish, which provided 99,97%V of their diet. The remaining 0,03%V was crustaceans which were found in the smallest fish from the Palmiet and Kleinmond estuaries. Only *A. breviceps* was identified in the diets of fish from the three estuaries and it provided 20%V overall. A major proportion of the diet in all three estuaries was unidentified pieces of fish. This shows that *P. saltatrix*, which has sharp interlocking teeth, can bite pieces off their prey, an ability which allows the consumption of prey items which would otherwise be too large to handle.

Previous descriptions of the stomach contents of *P. saltatrix* include those by van der Elst (1976), Smale & Kok (1983), Marais (1984) and Smale (1984). From these studies it is apparent that the diet of this species is similar in both the estuarine and marine environments with the general pattern as described above, i.e. smaller fish (< ± 200 mm) consume both crustaceans and fish but larger individuals consume almost entirely fish with cephalopods occasionally being important.

Psammogobius knysnaensis

Eight hundred and seventy-one guts of this species were examined of which 604 (69%) contained recognizable

food items, 222 from the Kleinmond and 191 each from the Bot River and Palmiet estuaries. The size range was 18–69 mm (Table 1).

This species is carnivorous with small invertebrates occurring in all the guts analysed and providing 94% of the total volume consumed (Table 3). Amphipods (66%O, 47%V), insects (45%O, 22%V) and polychaetes (26%O, 11%V) were the most important prey categories (Table 2).

The major difference in diet between samples in the three estuaries was that amphipods provided 74%V in the guts of the Palmiet sample but only approximately 30% in the other two estuaries. Almost all the amphipods consumed in the Palmiet were *G. bonnieroides* whereas in the Kleinmond *G. bonnieroides* and *M. zeylanica* were consumed and in the Bot River estuary *M. zeylanica* and *C. triaenonyx* were almost equally important species. The other notable difference in diets between the estuaries was that aquatic insect larvae (primarily chironomids) provided 37% and 35% of the volume consumed in the Kleinmond and Bot River but < 1% in the Palmiet estuary.

A summary of the diets of three size classes of *P. knysnaensis* from a single Bot River estuary sampling locality is given in Table 11. From this table it is evident that small invertebrates such as copepods (24%V) and ostracods (36%V) predominate in the small size class (< 30 mm) but are relatively unimportant to larger fish. The intermediate size class (30–50 mm) relied primarily on amphipods (40%V) and insect larvae (39%V) and larger fish (> 50 mm) on amphipods (42%V), decapods (22%V), insect larvae (16%V) and isopods (11%V).

Some evidence of seasonal differences in diet were apparent in all three estuaries sampled (Table 12). In the Bot River estuary six species provided more than 5% of

Table 11 The percentage composition (%V) of the major prey categories in the diets of three size classes of *Psammogobius knysnaensis* in the Bot River estuary

	Size class		
Prey category	< 30 mm	30–50 mm	> 50 mm
Polychaeta	5	5	6
Copepoda	24	2	–
Ostracoda	36	4	–
Isopoda	3	1	11
Amphipoda	27	40	42
Decapoda	–	1	22
Insect larvae	3	39	16

Table 12 The monthly contribution (%V) of important prey species in the diet of *Psammogobius knysnaensis* in the Bot River, Kleinmond and Palmiet estuaries. Species represented are those which contributed > 5% to overall volume

	Month											
Prey species	J	F	M	A	M	J	J	A	S	O	N	D
Bot River												
Ostracoda	7	1	2	1	–	14	–	12	9	9	2	6
Corophium triaenonyx	12	11	36	40	–	–	–	17	23	–	16	22
Melita zeylanica	31	55	18	32	–	4	–	23	20	10	6	16
Polychaeta	–	–	5	–	–	45	–	16	14	2	6	–
Chironomid larvae	12	10	14	12	–	11	–	5	25	68	25	18
Grandidierella bonnieroides	13	1	1	–	–	–	–	2	1	1	11	10
Kleinmond												
Ostracoda	1	–	1	2	2	7	2	45	24	2	1	2
Melita zeylanica	1	1	–	35	28	18	42	10	1	3	1	–
Polychaeta	26	17	10	–	41	15	8	47	26	1	31	28
Chironomid larvae	68	40	40	26	10	16	32	1	10	85	9	50
Grandidierella bonnieroides	3	22	38	8	9	40	2	1	3	2	55	10
Palmiet												
Ostracoda	–	–	2	2	40	26	20	1	2	–	–	–
Polychaeta	1	–	–	17	23	18	27	8	3	–	–	–
Grandidierella bonnieroides	93	96	95	73	9	25	9	68	88	79	91	97

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the total volume of food consumed throughout the year. Most polychaetes were taken between June and September, most chironomid larvae between September and November and most *G. bonnieroides* between November and January. *M. zeylanica* formed a substantial proportion of the diet between February and April but it was also important in other months. The contribution to the diet of the other two important categories, ostracods and *C. triaenonyx*, varied throughout the year. In the Kleinmond estuary the contribution of *M. zeylanica* was greatest from April to July and that of ostracods in August and September. The three other important prey categories (polychaetes, chironomid larvae and *G. bonnieroides*) showed no clear seasonal pattern. Only three categories provided > 5% of the total volume consumed in the Palmiet estuary. Ostracods and polychaetes provided their greatest contributions between April and July, and *G. bonnieroides* was overwhelmingly dominant for the remainder of the year.

Hanekom & Baird (1984) reported that *P. knysnaensis* in the Kromme River estuary fed on copepods, ostracods, isopods, amphipods, tanaids, cumaceans and annelid worms, a diet very similar to that reported above.

Rhabdosargus globiceps

Seventy-eight guts of *R. globiceps* were examined and 67 of them contained food, 19 from the Palmiet, 26 from the Kleinmond and 22 from the Bot River estuary. The size range of fish containing food was 28–192 mm in the Palmiet, 27–134 mm in the Kleinmond and 208–340 mm in the Bot River (Table 1).

Combined samples from the three estuaries indicated that algae (46%V), molluscs (23%V), decapods (20%V) and fish (8%V) were the main diet of this species (Table 2). There were, however, some differences in diet between the three estuaries. Isopods and amphipods, for example, provided approximately 5%V in the Palmiet but only 1–2%V in the Kleinmond and < 0,5%V in the Bot River estuary. Decapods which provided 38%V and 32%V in the Palmiet and Kleinmond estuaries provided only 18%V in the Bot River estuary. The opposite trend was true for molluscs, fish and algae, all of which were more important in the diet of the Bot River sample.

Sample sizes were too small to detect dietary changes with size or season but superficial examination of the data indicated that very small prey items such as copepods and ostracods were only present in fish of < 50 mm.

A detailed examination of the diet of juvenile *R. globiceps* in the Hermanus lagoon was provided by Talbot (1955). He found that this species consumed a wide variety of both 'hard' and 'soft' foods with filamentous algae occurring most frequently. Other common food items were amphipods, isopods and small gastropods. He also showed that very small fish (20–40 mm) fed primarily on planktonic organisms before diversifying to a wider variety of small invertebrate prey. Only when in excess of 100 mm did they start consuming 'hard' prey such as gastropods. No major changes in diet with season were reported.

Samples of guts of adult *R. globiceps* from the marine environment have been examined by Talbot (1955) and Buxton & Kok (1983). These authors show that small crustacea, bivalves, echinoids and polychaetes are the most important dietary components and that plant material is seldom consumed.

Rhabdosargus holubi

Sixty-five guts of *R. holubi* were examined of which 59 contained food, 14, 33 and 12 from the Palmiet, Kleinmond and Bot River estuaries respectively. The size ranges were 20–195 mm (Palmiet), 22–155 mm (Kleinmond) and 271–368 mm in the Bot River estuary (Table 1).

Approximately 59% of the volume of food consumed by *R. holubi* in the three estuaries was aquatic plant material and 41% invertebrates. The plant component comprised algae (primarily *Cladophora* sp. 26%V) and spermatophytes (primarily *Potamogeton* sp. 21%V). The invertebrate categories were molluscs, primarily *Hydrobia* sp. (20%V), and decapods, of which *C. kraussi* (16%V) was the most important species (Table 4). There was very little variation in diet between the three estuaries despite the large discrepancy in the size of the fish sampled. The four major food categories mentioned above provided 88–99% of the total amount of food consumed in the three estuaries and the only variation between them was that the contribution of vascular plants was smaller in the Palmiet estuary.

The diet of *R. holubi* has previously been examined by a number of authors. Blaber (1974) analysed guts from four eastern Cape estuaries and found that macrophytes and green algae provided an average of 81% of the diet with invertebrates, primarily amphipods, isopods and decapods, making up the remainder. Whitfield (1984) examined the guts of a similar size range (approx. 60–170 mm) in Swartvlei and showed that plants made up 55–72% of the diet, with *Musculus virgiliae* and *H. orbiculare* the only two important invertebrate species. The gut contents of smaller fish were examined from the Kromme estuary (Hanekom & Baird 1984), the Mhlanga estuary and Swartvlei (Whitfield 1985). In the Kromme estuary where the size range of fish examined was (20–60 mm) plants dominated the diet, whereas in the Mhlanga estuary and Swartvlei where fish of < 35 mm were examined there was no plant material and copepods, crustacean larvae, chironomid larvae and amphipods provided the bulk of the diet. Large individuals (> 150 mm) both in estuaries (Blaber 1974) and in the marine environment (Buxton & Kok 1983) consume primarily invertebrates with bivalves, polychaetes and decapods being the most important categories.

Sarpa salpa

The guts of six individuals of this species from the Bot River estuary were examined and all contained food. Algae, primarily *Cladophora* sp. and vascular plant material (primarily *Ruppia* sp.) occurred in all guts in approximately equal quantities and together provided over 99% of the contents. Very small amounts of insect

Table 13 The percentage composition (%V) of the major prey categories in the diets of three size classes of *Syngnathus acus* in the Bot River estuary

	Size class		
Prey category	< 70 mm	70–120 mm	> 120 mm
Copepoda	72	42	39
Isopoda	5	9	19
Amphipoda	21	46	39
Insect larvae	2	2	2

larvae and gastropods were also present.

The diet of this species in both the estuarine and marine environments has been described by a number of authors. Post larvae and small juveniles (< ± 20 mm) consume primarily copepods (Christensen 1978; Whitfield 1985) but larger fish feed almost exclusively on aquatic plants (Christensen 1978; Joubert & Hanekom 1980; Gerking 1984).

Syngnathus acus

This species was rare in the Palmiet and Kleinmond estuaries, consequently the entire sample for stomach content analysis was obtained from the Bot River estuary.

Small Crustacea were the only prey consumed (Table 3) and copepods (91%O, 43%V), amphipods (44%O, 42%V) and isopods (22%O, 13%V) were the only important prey categories. Within these categories *P. hessi* (27%V), *M. zeylanica* (27%V), *C. triaenonyx* (14%V) and *Exosphaeroma* sp. (8%V) were the most important species (Table 4).

Changes in diet with size were evident (Table 13). Copepods provided 71% of the volume consumed by the small size class (< 70 mm) but were less important in the diet of larger fish. Amphipods, on the other hand, although providing 21% of volume in the smaller size class, were twice as important to larger fish. The proportion of isopods increased with increasing fish size but insect larvae remained unchanged.

Day *et al.* (1981) reported that *S. acus* feeds on zooplankton, primarily copepods and amphipods. Hanekom & Baird (1984) reported that two specimens from the Kromme river estuary contained only macrurans.

Conclusions

The diets of some species varied between the three south-western Cape estuaries and between these estuaries and others elsewhere in South Africa. These differences were, however, usually quite small and involved changes only in the relative contribution of particular prey species or categories. For example the amphipod *G. bonnieroides* was common in the diets of carnivores in the Palmiet estuary but only occurred infrequently in samples from the Bot River estuary. The converse was true for *C. triaenonyx*. Omnivores consumed quantities of *Ruppia* sp. and *Potamogeton* sp. in the Bot River estuary but *Enteromorpha* sp., a species seldom found in the guts of fish from the Bot River estuary, was the only frequently consumed weed in the Palmiet estuary. These observed differences in diet between estuaries were never large enough to cause any doubt about the allocation of a particular species to a trophic category and there is evidence that they are attributable to differences in food availability. Branch & Day (1984) provide data that shows *G. bonnieroides* and *Enteromorpha* sp. to be common and *C. triaenonyx*, *Ruppia* sp. and *Potamogeton* sp. to be rare or absent from the Palmiet estuary whereas Koop *et al.* (1983) and de Decker & Bally (1985) who sampled the Bot River estuary show the opposite.

A striking feature of the dietary data presented here is that fish of < ± 30 mm, regardless of species, all consume minute invertebrates, primarily zooplankton. The importance of zooplankton in the diets of postlarval fish has been examined by Whitfield (1985). He reviews literature that shows zooplankton to be the major nutritional resource of larval and postlarval fish in most aquatic environments and suggests that this is due to the higher energy value of zooplankton relative to other organisms of equivalent size. He considered that consumption of alternative food by fry would occur only where zooplankton stocks are low relative to other detritus based food resources, a situation common in South African estuaries.

When larger than ± 30 mm the fish developed considerably more diverse diets and most of the species specialized to some extent. Two of the species became primarily herbivorous, five became detritivorous, seven remained carnivorous, three became omnivorous and two became piscivorous. When these categories of food are compared with available resources (from data provided by Koop 1982; Koop *et al.* 1983; Branch & Day 1984; de Decker & Bally 1985) it is apparent that the whole spectrum of available food is utilized by the fish fauna.

If Whitfield (1985) is correct in arguing that fry will benefit from eating only zooplankton, then the consumption of less energy rich invertebrates (such as amphipods) by the fish species sampled in this study suggests that zooplankton may be in short supply. A similar line of thought could also be used to explain the consumption of large quantities of plants by the three omnivores, *R. globiceps*, *R. holubi* and *L. lithognathus*. The diets of these species change from zooplankton in fry (< 30 mm) to primarily small invertebrates (when the fish are 30–100 mm) and then to a mixture of small invertebrates, larger invertebrates and weed. In the marine environment these species eat almost entirely invertebrates (Talbot 1955; Mehl 1973; Buxton & Kok 1983). When one considers that plant material is less digestible and energy rich than invertebrates (Brett & Groves 1979) this might suggest that the consumption of weed in estuaries occurs because the larger size classes of invertebrates are not available in sufficient quantities.

The existence or intensity of competition between fish species, and whether or not food is in any way limiting, cannot be ascertained from the data presented in this

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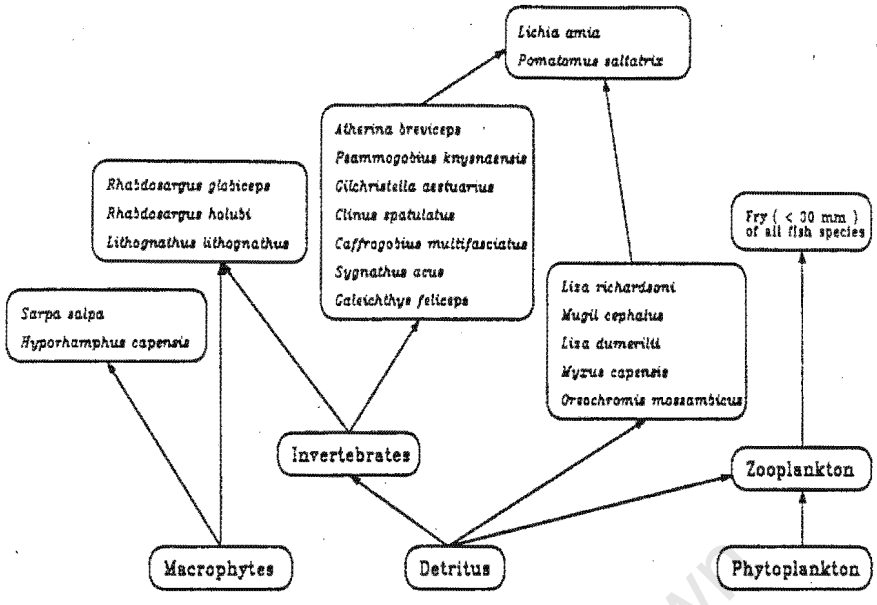

Figure 2 A summary of the most important trophic links betwen fish species common in the Bot River, Kleinmond and Palmiet estuaries in the south-western Cape.

paper. Only when details of the mechanisms of resource partitioning between species have been elucidated and when the total annual production of the food resources and consumption by the fish community are available, will a greater understanding of the trophic inter-relationships within south-western Cape estuaries be possible.

Trophic relationships between the fish species examined in this study are summarized in Figure 2. There were three primary sources of food: phytoplankton, aquatic macrophytes and detritus. None of the fish species examined consumed significant amounts of phytoplankton although this food source may have been of some importance in supporting the fry of all species via zooplankton. Macrophytes were consumed directly by the two herbivores and formed a significant proportion of the diets of the three omnivores. The major proportion of the south-western Cape fish population, however, relied either directly or indirectly on detritus, a feature that it has in common with estuarine fish populations elsewhere in South Africa (Day *et al.* 1981) and worldwide (Odum, Zieman & Heald 1972; Carr & Adams 1973; Fagade & Olaniyan 1973).

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CHAPTER 12.

A COMPARISON OF THE PHYSIOLOGICAL CONDITION OF THE SOUTHERN MULLET *LIZA RICHARDSONI* (SMITH), IN A CLOSED ESTUARY AND THE SEA

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SUMMARY

The physiological condition of the mullet, *Liza richardsoni* (Smith), from the closed Bot River estuary is compared with that of the same species from False Bay. Levels of protein, lipid, water and ash, as well as energy content were determined in fish from the two environments. Protein (17,94% *vs.* 18,53%) and ash levels (3,41% *vs.* 4,81%) were similar in both estuarine and marine fish. Lipid (9,95% *vs.* 2,23%) and energy levels (18,35 kJ g^{-1} dry weight *vs.* 14,18 kJ g^{-1} dry weight), were significantly higher, while levels of water (67,73% *vs.* 74,87%) were lower in the estuarine fish. On average the estuarine *L. richardsoni* were in better condition than their marine conspecifics.

Liza richardsoni does not spawn in estuaries and their better condition in the estuary could possibly be attributed to the retention of energy usually lost through spawning in the sea. On the other hand, estuarine subadults were already in an improved condition, which could only be due to better feeding conditions. It is therefore concluded that estuarine *L. richardsoni* can maintain a better condition due to both more favourable feeding conditions and the retention of energy usually lost through spawning.

INTRODUCTION

Estuaries have long been known to be organically rich in comparison with marine coastal systems (Odum & De la Cruz 1967, Head 1976, Day 1981). Many South African estuarine fish species are marine migrants, presumably utilising the abundant food sources available in estuaries (Blaber 1981, Day *et al.* 1981). Since the condition of fish has been directly related to their food selection (Blaber 1975), it follows that if estuarine fish benefit from the richer feeding grounds, they should be in better physiological condition than their marine conspecifics. This, however, has not yet been shown by a direct comparison of estuarine and marine fish populations.

The commercial importance of mullet (Mugilidae) has given rise to a large literature on their physiological condition. Attention has generally focussed on the grey mullet, *Mugil cephalus* (Linnaeus), since it is cultured in many parts of the world. Chemical analyses of the tissues of this species are readily available (for reviews see: Thomson 1966, Love 1970, 1980), but no comparisons between marine and estuarine mullet could be found.

Relatively few studies have dealt with the southern mullet, *Liza richardsoni* (Smith), since it has a limited range, extending from Moçamedes, in southern Angola, to Transkei, on the east coast of the Republic of South Africa (Penrith 1978). Marais (1976) and Marais & Erasmus (1977) reported analyses of *L. richardsoni* caught in the Swartkops Estuary near Port Elizabeth, but did not include comparisons with marine mullet. As far as could be ascertained, their study and that of Van Wyk (1944) are the only analyses of *L. richardsoni* published to date.

In this paper, the physiological condition of estuarine and marine *L. richardsoni* is compared in order to determine whether richer feeding areas contribute to better condition in estuarine mullet.

Estuarine *L. richardsoni* were obtained from the Bot River estuary, near Kleinmond on the south-west coast of South Africa (34°20′S 19°06′E). A detailed description of the estuary may be found in Koop *et al.* (1983). Pertinent to this study is the fact that the estuary is normally separated from the sea by a sand barrier, but that at high water-level, a natural overflow channel opens to the sea via the swamps at Kleinmond. Due to the water-releasing effect of this channel, the sand barrier is seldom breached naturally, and at the time of sampling (April 1981), the estuary had been closed for four years (1977–1981). Since the overflow channel allows only limited recruitment of fry at times of high water-level, the estuarine *L. richardsoni* were effectively trapped inside the estuary during this four-year period. This afforded the ideal opportunity for comparison with marine mullet, which was caught in False Bay, approximately 50 km west of the Bot River estuary.

MATERIALS AND METHODS

Collection of samples

Samples of estuarine *L. richardsoni* were obtained in April 1981 in the Bot River estuary, using a small seine net (25 m × 2 m; 10 mm stretched mesh) and braided nylon gill nets (760 m × 2,2 m; 8 mesh sizes ranging from 35 mm to 197 mm stretched mesh). In False Bay, marine fish were caught by dragging the small seine net at St James and Fish Hoek beaches (34°07′S 18°28′E) to catch juveniles and fry, while larger fish were obtained from commercial treknet fishermen at Strandfontein (34°05′S 18°40′E). All fish were measured (total length: TL) and assigned to one of seven 60 mm size-classes (0–420 mm). They were frozen immediately thereafter and stored at −20 °C until processed.

The abundance of fish of various size-classes differed in the Bot River estuary and False Bay. In the estuary, the fish of the smaller size-classes (TL <180 mm) were scarce, while in False Bay no fish of the two largest size-classes (TL >331 mm) were caught.

Analyses of body composition

Since the proportions of body constituents vary in different parts of the body (Suppes *et al.* 1967), whole fish were used in composition analyses. After the contents of their alimentary canals had been removed, fish were homogenized together in each size-class. The larger size-class (TL >180 mm) were represented by three randomly selected fish, while all the fish in the smaller size-classes were homogenized. Fish were minced in a Spong no. 5 meat mincer and after thorough mixing, homogenized with an Ultra-Turrax homogenizer. Homogenates were stored at −20 °C until processed further.

Subsamples of the homogenates of each size-class were analysed for protein, water, lipid and ash levels (expressed as % of total wet weight), as well as for energy

content (expressed as kJ per gram dry weight). The levels were determined in the following ways:

(i) protein: subsamples were analysed for total protein (total nitrogen × 6,25) by the micro-Kjeldahl method (Kirk 1947).

(ii) water: levels were determined as weight loss from preweighed subsamples, oven-dried at 65 °C to constant weight.

(iii) lipid: total lipids were determined in subsamples by a method adapted from Bligh & Dyer (1959), using methanol and chloroform as extraction solvents.

(iv) ash: subsamples were ashed for 5 hours in a muffle furnace at 450 °C.

(v) energy: subsamples of approximately 0.5 g dry weight were analysed in a Gallenkamp bomb calorimeter.

RESULTS

Body composition

Table 1 gives the levels of the four body constituents and the energy content in each size-class. The levels of protein were generally similar in both estuarine and marine mullet, while ash levels were higher in the marine fish, possibly due to their sandier feeding substrate. Differences in the levels of lipid, water and energy, however, were more pronounced between the two stocks. Lipid levels were higher in all the estuarine mullet, with the biggest variations (up to 15%) occurring in the larger size-classes. Energy-content followed the same trends, with differences of up to 7 kJ g^{-1} dry weight. The opposite was true for the water-levels, which were higher in all but one of the size-classes of marine mullet. The biggest variations in the water-levels (up to 14%) were again found in the larger mullet.

Significant negative correlations exist between lipid and water-levels ($r = -0,99$; $p<0,001$), as well as between energy-content and water-levels ($r = -0,97$; $p<0,001$) in the estuarine mullet. A significant positive correlation was found to exist between the lipid and energy-levels ($r = +0,98$; $p<0,001$) in the estuarine fish. None of these constituents were significantly correlated in the marine mullet.

Changes in composition with length

It is clear from Table 1 that there are far greater variations in lipid, water and energy between size-classes in the estuary than in the sea. Figure 1 illustrates the changes in body constituents with length in the mullet from the two environments. It is apparent that the increase in lipid in the larger size-classes of estuarine fish is associated with a relative decrease in protein and ash-levels (Fig. 1A).

The changes in lipid, energy and water with length can be more readily compared in Figures 2, 3 and 4. Levels of significance were determined using Student's t-test. It can be seen that while lipid, energy and water are significantly correlated with length in the estuarine mullet, only energy is significantly correlated with length in the marine mullet. The regressions of length *vs.* lipid and water-levels in the marine mullet are not significant, but are included in Figures 2 and 4 to facilitate comparison.

The differences between the estuarine and marine *L. richardsoni* are clear. The

Table 1

Levels of body constituents (% of total weight) and energy, E (kJ per gram dry weight) in *Liza richardsoni* from the Bot River estuary and False Bay. Mean values, standard deviations (SD), and numbers of determinations (N)

Size-Class (mm)	Protein (%)	SD	N	Lipid (%)	SD	N	Water (%)	SD	N	Ash (%)	SD	N	E (kJ g^{-1}dw)	SD	N	Total
Bot River																
61	18,00		1	3,04		1	72,87	0,49	2	3,71	0,04	3	14,97	0,23	2	97,62
61–120	17,29	0,47	3	2,75	0,15	2	76,13	1,46	2	3,78	0,88	3	14,50	0,62	2	99,95
121–180	18,07	0,14	3	8,11	0,03	2	70,35	0,50	2	3,19	0,54	3	17,43	0,21	3	99,72
181–240	18,77	0,11	2	8,17	0,63	4	69,40	0,30	2	3,39	0,29	3	18,50	0,21	4	99,73
241–300	17,31	0,15	3	16,68	0,85	3	60,60	1,41	2	3,13	0,27	3	21,15	0,22	4	97,72
301–360	17,35	0,11	3	16,86	0,31	3	61,62	2,41	2	3,60	0,21	3	21,50	0,64	4	99,43
361–420	18,77	0,06	2	14,01	0,20	4	63,17	0,91	2	3,09	0,44	3	20,43	0,33	4	99,04
Mean	17,94	0,65		9,95	6,00		67,73	5,99		3,41	0,29		18,35	2,86		
False Bay																
61	17,58	0,25	3	2,68	0,03	3	75,55	0,14	2	4,73	0,66	3	13,80	0,61	3	100,54
61–120	17,49	0,14	3	1,79	0,05	3	75,84	0,01	2	5,37	0,78	3	13,95	0,81	4	100,49
121–180	19,25	0,26	3	2,11	0,12	3	74,19	0,22	2	4,50	0,33	3	14,32	0,17	4	100,05
181–240	19,08	0,20	3	1,78	0,02	3	74,54	0,92	2	4,81	0,67	3	14,17	0,43	4	100,21
241–300	19,23	0,26	3	2,80	0,09	3	74,24	0,47	2	4,63	0,17	3	14,66	0,36	4	100,90
Mean	18,53	0,91		2,23	0,48		74,87	0,77		4,81	0,33		14,18	0,33		

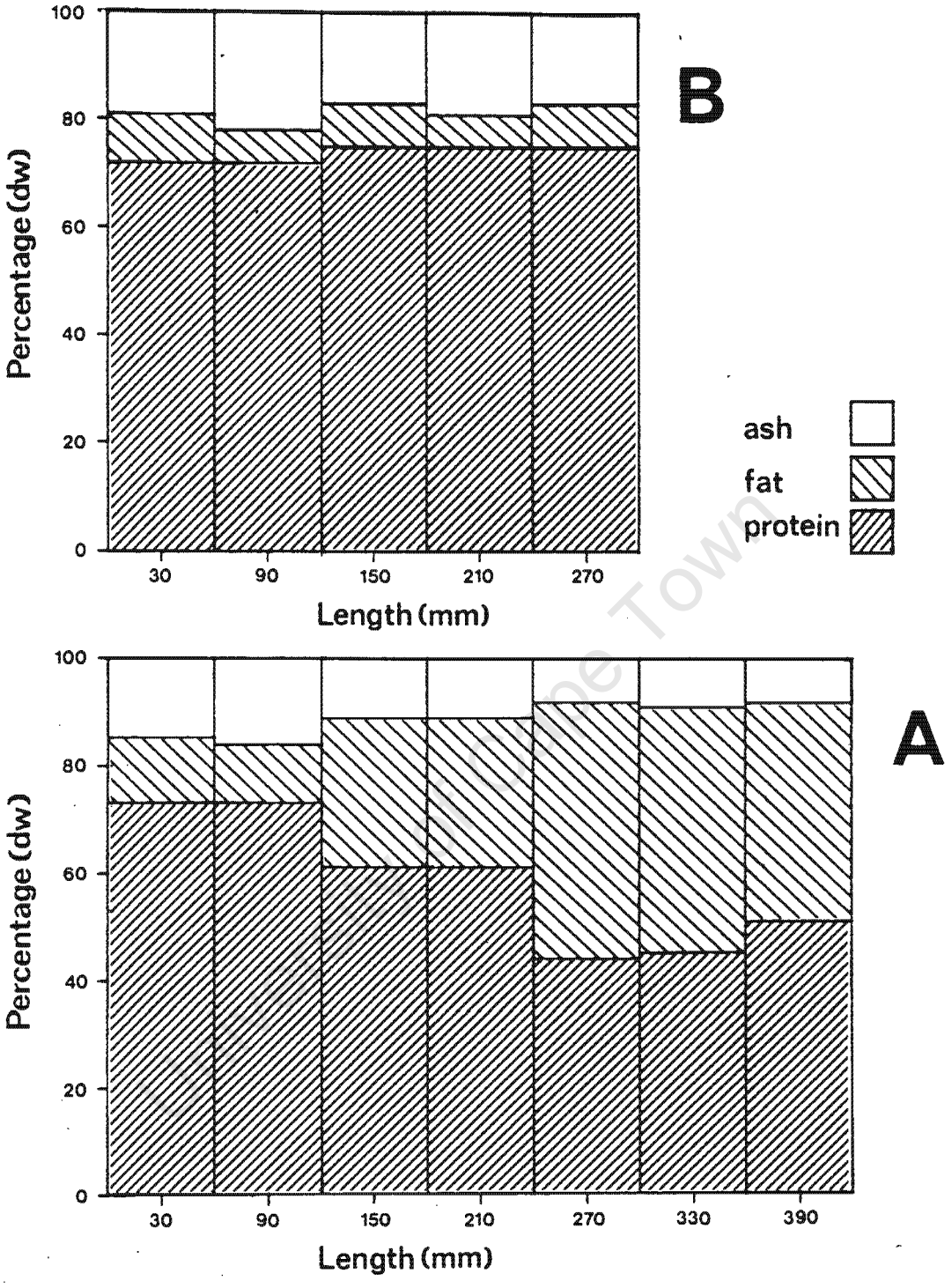

Fig. 1. Changes of body constituents with length in the various size classes of *Liza richardsoni* in the Bot River estuary (A) and False Bay (B), expressed as percentage of the dry weight.

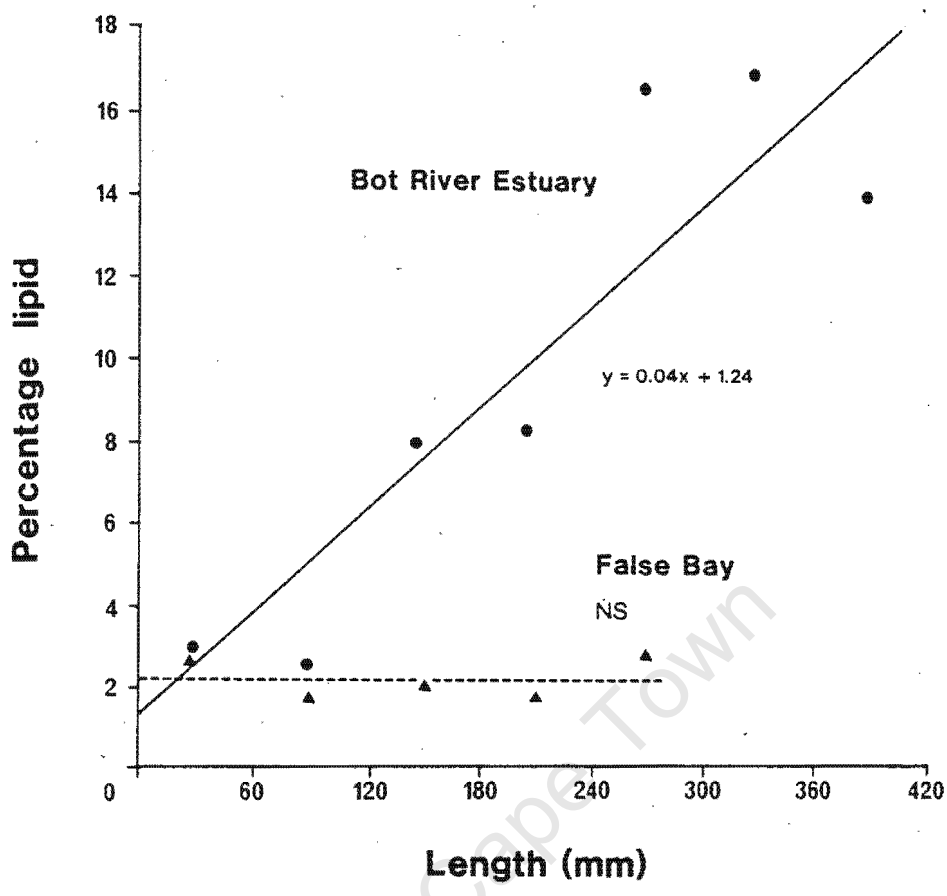

Fig. 2. The relationships between length and percentage lipid content in *Liza richardsoni* from the Bot River estuary (●) and False Bay (▲). For the Bot, $r = 0.89$ $p<0.01$; for False Bay, r is not significant (NS).

large increases in lipid-levels (Fig. 2) and energy-content (Fig. 3) as well as the decrease in water-levels (Fig. 4) with length in the estuarine mullet are not present in the marine mullet. Figures 1 to 4 also illustrate the similarities between estuarine juveniles (TL <120 mm) and marine mullet of all size-classes. This is particularly evident in Fig. 1. It is important to note, however, that estuarine subadults (TL 120–220 mm) have significantly higher lipid and energy-levels than the estuarine juveniles (Lord's Range test, $p<0,05$), and that these levels are, in turn, significantly higher in the estuarine adults (TL >220) than in the subadults (Lord's Range test, $p<0,05$).

DISCUSSION

The results of chemical analyses of body constituents of marine and estuarine *L. richardsoni* indicate that larger estuarine mullet are in better condition than their marine conspecifics. Generally, the body-constituent levels given by Marais & Erasmus (1977) for *L. richardsoni* in the Swartkops estuary are similar to those found in the present study for estuarine mullet, while the levels reported by Van Wyk (1944) for muscle fillets of marine *L. richardsoni* correspond to those found for marine mullet.

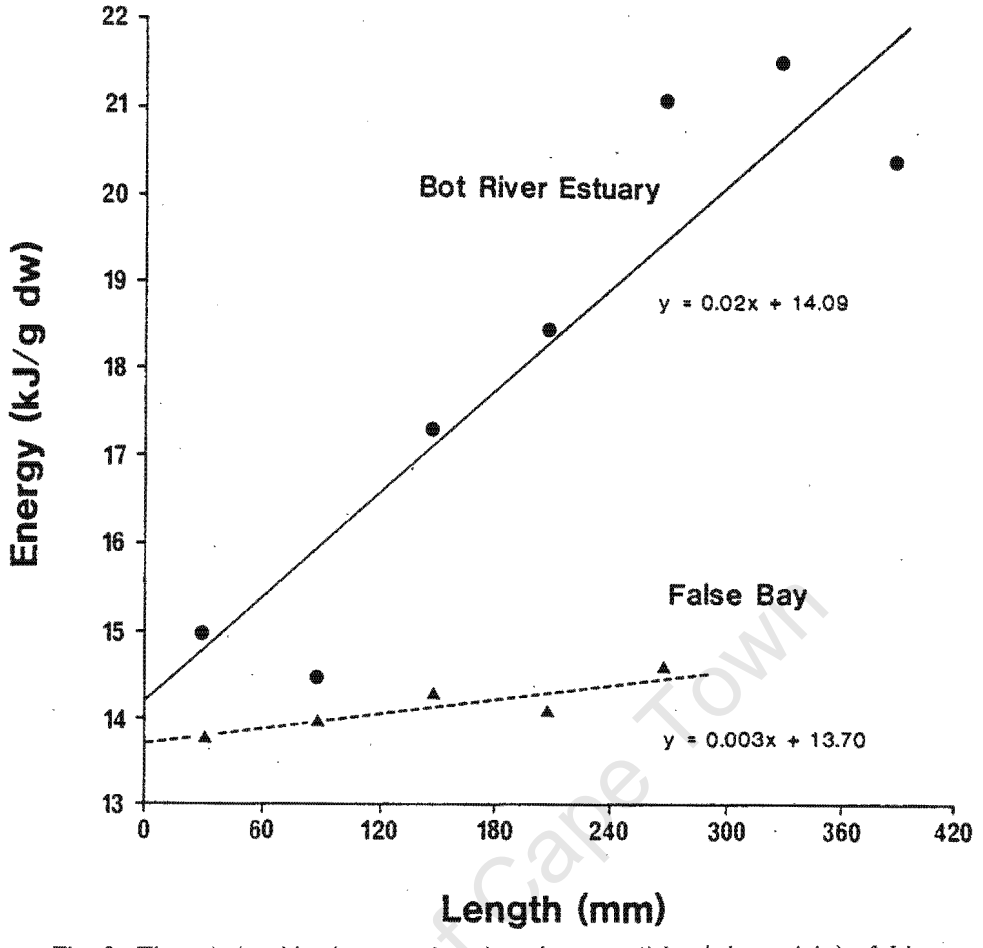

Fig. 3. The relationships between length and energy (kJ g^{-1} dry weight) of *Liza richardsoni* from the Bot River estuary (●) and False Bay (▲). For the Bot, $r = 0{,}92 \pm <0{,}005$; for False Bay $r = 0{,}88$ $p < 0{,}05$.

The migrations of many mullet species in and out of estuaries are well known (Wallace 1975, Wallace & Van der Elst 1975, Blaber & Whitfield 1977, Blaber & Blaber 1980). *Liza richardsoni* spawns in the sea (Lasiak 1983) and the fry may migrate into estuaries, where they remain until adolescence, having to return to the sea to spawn (Blaber 1981, Wallace *et al.* 1984). At the time of sampling for this study, however, the Bot River estuary had been closed for four years (1977–1981). This interrupted the normal migration patterns, preventing the mullet trapped inside from spawning during that period. Recruitment of a limited number of fry and juveniles was possible via the overflow channel to Kleinmond (Bennett *et al.* 1985). The absence of spawning, as well as low recruitment, was evident from the difficulty experienced in catching the smaller size-classes. No ripe and running *L. richardsoni* were caught in the estuary during the same period.

Marais & Erasmus (1977) report that *L. richardsoni* feeds mainly on organic debris, and both planktonic and attached diatoms. Estuaries are therefore ideally suited to mullet, since these food items are present in abundance (Blaber & Whitfield 1977).

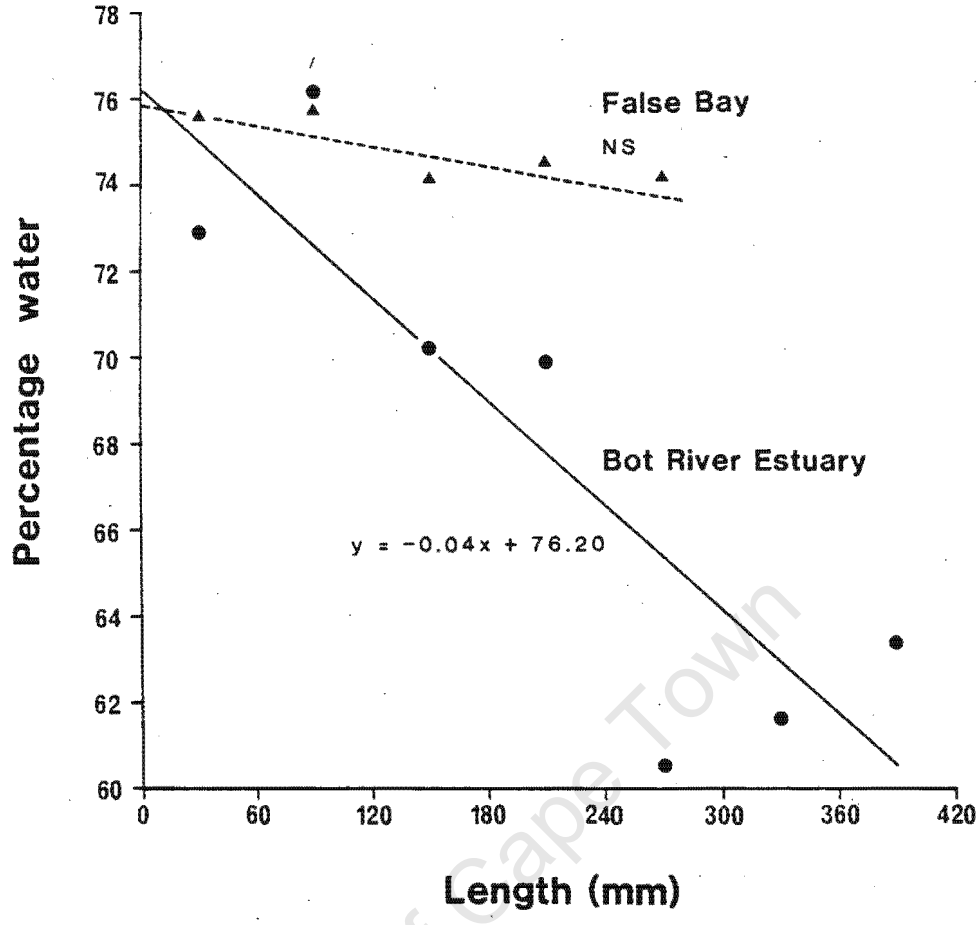

Fig. 4. The relationships between length and percentage water content in *Liza richardsoni* from the Bot River estuary (●) and False Bay (▲). For the Bot, $r = -0{,}87$ $p<0{,}001$; for False Bay r is not significant (NS).

The 'balance of body constituents' of fish is related to their food intake and energy expenditure (Brett *et al.* 1969). Lipid content and condition of *Rhabdosargus holubi*, for example, have been shown to be positively related to feeding level (Blaber 1975). It seems therefore that the higher lipid and energy-levels found in subadult *L. richardsoni* from the Bot River estuary may be attributed to more favourable feeding conditions. Estuarine adults, moreover, had significantly higher lipid and energy-levels than the subadults. Mullet are known to have maximum lipid levels in the pre-spawning season (Deng *et al.* 1976). As spawning never actually takes place inside the estuary, the pre-spawning levels are apparently maintained. It is thus concluded that both the favourable feeding conditions, as well as the absence of spawning, contribute to the higher fat and energy content of the mullet in the Bot River estuary.

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CHAPTER 13.

RELATIONSHIPS BETWEEN PRODUCTION AND CONSUMPTION OF PREY SPECIES BY RESIDENT FISH IN THE BOT, A COOL TEMPERATE SOUTH AFRICAN ESTUARY.

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Data on the biomass, diets, feeding cycles and consumption rates of the resident fish of the Bot estuary are presented, together with figures for the biomass and production of invertebrates. These data are used to quantify the impact of the fish on their prey populations and to examine how the fish apportion their food resource. Calculations of total daily consumption by the six resident predatory fish species ranged from 3.48% to 5.66% body mass d^{-1} and their combined annual consumption was 5.99 g m^{-2}. The total standing stock of potential prey was 7.1 g m^{-2} and total annual production was calculated as 35 g m^{-2}. Consumption by the fish therefore accounted for 17% of secondary production, or 30% of the production by prey species, suggesting that predation by fish was not likely to be having a major impact on the prey resource and that food was not in short supply. A few species do, however, have a substantial proportion (>80%) of their production consumed by fish. Most of the fish consumed a wide variety of prey but there was considerable subdivision of diet with no two species sharing their most important prey category. Dietary niche width for the different species was significantly correlated with their abundance but not with their average overlap with the other species, implying that the most successful species are those with the broadest niches and that specialisation is a dubious means of reducing competition.

INTRODUCTION

It is now well established that many marine fish use estuaries during their juvenile stages and that a different suite of fish remains resident in estuaries throughout their lives (Hedgepeth, 1967; Day *et. al.*, 1981; Potter *et. al.*, 1986). The latter species are often relatively small but can achieve considerable densities and biomass. There are at least three reasons why estuaries should be favourable to both groups of fish: they may provide shelter from physical stresses, including wave action; protection from larger predatory fish and other marine predators; and a food supply which is richer and more predictable than that in the open sea.

The first possibility - that estuaries provide shelter from physical stress - is the least likely, considering that estuaries are at times physically stressful, being subject to unpredictable flooding and salinity stress, often associated with mass mortalities of fish (Blaber & Whitfield, 1976; Bennett, 1985). Furthermore, the juveniles of many marine fish are able to survive and even preferentially occupy the wave-beaten shallows of sandy beaches (Modde, 1980; Lenanton, 1982; Lasiak, 1986; Bennett, 1989a).

There is some evidence, albeit circumstantial, to support the second suggestion - that estuaries provide a shelter from predators. Fish have been shown to prefer turbid estuaries and, under experimental conditions, to avoid clear water (Blaber & Blaber, 1980; Cyrus & Blaber, 1987a,b). Small fish often concentrate in weed-beds (Heck & Orth, 1980; Whitfield, 1984). Both phenomena have been ascribed to avoidance of predators (Blaber & Blaber, 1980; Lenanton, 1982), although this remains to be tested.

The third posssibility - that estuaries provide a rich source of food - is not easy to test experimentally because of the mobility of fish but, again, there is indirect

shallows and are associated with the major concentrations of benthic invertebrates and resident fish, including one species, *Clinus spatulatus*, endemic to the system.

In this paper we document the numbers and biomass of fish in the Bot Estuary during the prolonged periods when it is closed, and recapitulate their diets (previously recorded in in more detail in Bennett, 1989c). We also describe the diurnal feeding cycles and rates of gut clearance of the resident carnivorous fish, from which it is possible to calculate their feeding rates. We then compare their rates of consumption against the productivity of their prey species, using published information on the species composition and biomass of the benthic invertebrates (Koop *et. al.*, 1983; de Decker & Bally, 1985) and standard conversions to productivity (Banse & Mosher, 1980). One of the advantages of using the Bot estuary to answer questions of this nature is that it is isolated from the sea for prolonged periods, so that calculations of production and consumption are not complicated by import and export. Another is virtual absence of other predators which might influence the prey of fish. Waders do feed at the Bot, but their numbers are relatively low because the system is nontidal while closed, and they are confined to a narrow fringe and so do not impinge on the distribution of the fish.

While our primary objective is to quantify the impact of fish on their prey and the excess (if any) of prey production over consumption, the research has broader implication. In particular, it allows exploration of the extent to which fish apportion their niches, both in terms of dietary overlap and habitat use. Several other papers have adopted this approach to test if fish partition their food or habitats (e.g. Helfman, 1978; Macpherson, 1981) as a means of avoiding competition. Schoener (1982) provides a general review of the philosophy behind this approach. Our data do not allow an explicit test of whether the fish are competing. They do, however, permit an indirect attack on the question of whether "apportionment" is necessary to avoid competition, whether specialisation of diet leads to a reduction of overlap

evidence favouring it. Several studies have shown that subtidal estuarine predators are unlikely to deplete their prey (Paine, 1980; Raffaelli & Milne, 1987), and de Decker and Bennett (1985) have shown that mullet (*Liza richardsoni*) trapped in estuaries maintain better condition than those living at sea.

In this paper we focus on the interaction between resident fish and their prey in a cool-temperate estuary, the Bot Estuary, situated on the southwestern Cape coast of South Africa (Figure 1). The estuary has been the subject of considerable research, including work on the extent and productivity of its weed beds (Bally *et. al.*, 1985), zooplankton (Coetzee, 1985), densities and biomass of benthic invertebrates (Koop *et. al.*, 1983; de Decker & Bally, 1985; de Decker, 1987), avian predators (Heyl & Currie, 1985) and fish populations (Bennett, 1983; Bennett *et. al.*, 1985; Bennett, 1989b).

Briefly, the most important features are as follows. The system is closed to the sea most of the time, except for occasional natural breachings when floods occur (three times in the past fifty years) and more frequent man-induced breachings (about every three to four years) when rising waters threaten the surounding land. After the mouth is breached, it remains open for two to four months before being closed once again by the build-up of wave-deposited marine sand. While the mouth is closed, the estuary becomes gradually more saline during the dry summer and then more fresh with winter rains. Because it is connected to an adjacent estuary by natural spill-over, water is diverted as levels rise during winter. This has two important consequences. Firstly, levels seldom reach the point at which they naturally breach the mouth. Secondly, marine water cannot penetrate, but freshwater is progressively added and slowly dilutes the estuary. Were it to be left to its own devices, it would probably become a coastal freshwater lake, but, because of periodic artificial breachings, it is maintained as an estuary. While the mouth is closed, dense weed-beds (mostly of *Ruppia* and *Potamogeton*) build up in the

with other species, and whether specialisation is a successful option if it is gauged in terms of the relative abundance achieved by different species.

METHODS

The fish community.

Data concerning the species composition, occurrence, abundance, biomass and life cycle characteristics of the fish in the Bot estuary were obtained from Bennett (1989b). In brief, a 25m long seine net with a stretched mesh size of 10mm was employed to sample the fish, sweeping on average an area of $525m^2$ per sample. Three sites, all situated in the shallow weeded margins around the estuary, were sampled monthly over a 13 month period between April 1980 and April 1981 (Figure 1). Density (N m^{-2}) and biomass (mg m^{-2}) were calculated as total catch / total area sampled. Further details of sampling and the characteristics of the fish community inhabiting the estuary are recorded by Bennett (1989b).

Diets of the fish.

The composition of the fish diets was obtained from Bennett (1989c). Samples of fish (N = 38 to 351) for analysis of stomach contents were selected so as to cover the full available size-range of each species. The amounts of different prey taxa in the fish stomachs were converted from settled volume to wet mass assuming $1mm^3$ = 1mg, and then to dry mass using the relationships in Field *et. al.* (1980).

Niche width and overlap.

The formula of Levins (1968), $B=(\sum p_i^2)^{-1}$ (where p_i is the proportional use of prey item i in the diet of a species), was used to calculate the dietary niche widths (B). As the value of B ranges from 1 to a maximum of n, the number of food categories present, B was standardised to B_S, which ranges from 0-1, to facilitate comparisons

between species: B_S = B-1/n-1 (Evans, 1983). The overlap in diet (C) between pairs of species (x and y) was calculated as $C_{xy} = \sum \min(p_{xi}, p_{yi})$, where a value of 0 for C_{xy} indicates no overlap and 1 indicates complete overlap (Hurlbert, 1978).

Feeding periodicity and daily consumption.

Feeding periodicity was established by quantifying the amount of food (as a percentage of dry body mass) in the guts of subsamples of 5-10 fish of each species taken at 3-hourly intervals over three separate 24-hour periods. Seasonal effects such as photoperiod and temperature were compensated for by conducting sampling in June, February and September and by combining data collected during corresponding 3-hour periods at different times of the year. Daily food consumption was estimated by applying the 24-hour feeding data to the Elliot and Persson (1978) model for cyclic feeding and elimination: $ds/dt = I_{(t)} - ks$, where s is the food content of the stomach (% fish body mass) at time t, $I_{(t)}$ is the feeding rate at time t (% fish mass h^{-1}) and k is the instantaneous elimination rate (h^{-1}). This model assumes that the elimination rate is proportional to stomach content, that feeding and digestion follow a stable cycle of constant period (r), that $I_{(t)}$ is constant at Ic during the feeding portion of the cycle and zero for the non-feeding period. It further assumes that the population has uniform Ic, k and r which are synchronous in cycle.

The general solution for this model and its equations, and details of how 24-hour feeding-data are fitted to the model, are given by Lane *et. al.* (1979). Solution of the equations for the two portions of the cycle (feeding and elimination) yield values for Ic and the duration of the feeding period which, when multiplied, give an estimate of daily ration.

Invertebrate standing stock and production.

Quantitative surveys of the benthic macrofauna in the Bot estuary have been

conducted by Koop *et. al.* (1983) and de Decker and Bally (1985). Both studies were undertaken when the estuary had been closed for at least two years. Koop *et. al.* (1983) presented their standing stock data in sufficient detail to allow the extraction of samples taken in the submerged marginal weedbeds within 50m of the shore and where sampling of the fish took place (Figure 1). De Decker and Bally (1985) only present average standing stocks of the different species over the whole estuary, but since only seven of the 27 samples that they took were in the "deep zone" which was devoid of macrophytes, these data were considered relevant to this study. The location of these sampling sites is shown in Figure 1. Standing stocks used here are average values (mg dry m^{-2}) of the two studies combined. Zooplankton standing stocks were taken as the average value obtained by Coetzee (1985) over the whole estuary between July 1980 and August 1981, during which time the estuary was closed.

No direct measures of production of any of the prey species consumed by fish in the Bot estuary have been made and the lack of details on the lifespans of the majority of species precluded the use of the relationship between productivity and lifespan calculated by Robertson (1979). However, the mass at maturity, or at least adult body mass, of all prey except insect larvae was established from samples taken in the field. This allowed the use of the relationship between mass at maturity (M_S) and P/B ratio established by Banse and Mosher (1980). This relationship, $P/B = 0.65\ M_S^{-0.37}$, required the conversion of M_S from mass to kcal which was done using the conversions given by Field *et. al.* (1980). The P/B ratio of insect larvae was estimated by using the energy value for larvae immediately prior to metamorphosis rather than M_S.

RESULTS

Monthly seining in the Bot estuary resulted in the capture of the 14 fish species listed in Table 1. The six species first listed in Table 1 accounted for 99% of the total number of fish caught, and most of the calculations in this paper have been based on these species. All were small species which resided in the marginal weed beds throughout the year and all were carnivorous. The remaining eight species were not considered primarily because they were not important consumers of weed-bed invertebrates (Bennett, 1989c) or because they occurred infrequently in the catches and in small numbers, suggesting that they were not an important component of the invertebrate-eating fauna of the weeded areas. This contention is supported by their greater abundance in gill net catches in deeper, offshore, non-weeded areas (Bennett *et. al.*, 1985) and their largely detrital or piscivorous diets (Bennett, 1989c).

Details of the diets of the six fish species are provided in Table 2. It is evident that most of the fish consumed a wide variety of prey with categories such as copepods, ostracods, amphipods and insect larvae being consumed by all the species. There was, however, considerable subdivision of diet between species with no two fish sharing their most important prey. The most important prey of *Atherina breviceps*, *Gilchristella aestuaria*, *Caffrogobius multifasciatus*, *Clinus spatulatus*, *Psammogobius knysnaensis* and *Syngnathus acus* are, respectively, amphipods (26.59% dry mass), ostracods (32.55%), fish (34.27%), gastropods (45.13%), insect larvae (44.47%) and copepods (57.23%). *Atherina breviceps* had the greatest index of niche width (0.36) while *S. acus* (0.07) was the most specialised feeder.

The diet of *A. breviceps*, the species with the widest feeding niche, overlapped considerably with all other species (Table 3) and that of *P. knysnaensis* overlapped quite markedly with *C. multifasciatus* and *G. aestuaria*, primarily because these three

species consumed considerable quantities of insect larvae. There was little overlap amongst the other species.

Round-the-clock sampling showed that two species fed at night (*A. breviceps* and *P. knysnaensis)*, three species during the day, (*G. aestuaria*, *C. spatulatus* and *S. acus*), and that *C. multifasciatus* fed at dawn and dusk (Figure 2). The amounts of food in the stomachs of these species throughout the 24 hour cycles allowed calculation of total daily consumption by each species (Table 4). These estimates ranged between 3.48% dry body mass per day for *C. multifasciatus* and 5.66% b.m. d^{-1} for *G. aestuaria*. Knowing the densities each fish species, annual consumption by the six species could be calculated, and totalled 5.99g.$m^{-2}y^{-1}$ with 5.09g.$m^{-2}y^{-1}$ being consumed by *A. breviceps* (Table 4).

Approximtely 40 invertebrate and 6 resident fish species were recorded in the Bot estuary during the surveys of Koop *et. al.* (1983), de Decker and Bally (1985), Coetzee (1985) and Bennett *et. al.* (1985). The total standing stock of these potential prey species was approximately 6.9g m^{-2} (Table 5). Only approximately 25 species were identified in the stomachs of the fish, and together their standing stock was 3.9g m^{-2} i.e. 55% of the total. This discrepancy between the total standing stock and the standing stock of those species that were consumed is largely attributable to the absence of *Arcuatula capensis* (2.6g m^{-2}; 37% of biomass) from the diets of the six species of fish considered here. The remaining prey species that were not consumed accounted for less than 10% of biomass.

A knowledge of the adult masses of the prey species allowed an estimate of their production by using the relationship of Banse and Mosher (1980) to obtain P/B ratios (Table 5). Total production was calculated to be approximately 35g $m^{-2}y^{-1}$, 20g $m^{-2}y^{-1}$ being provided by the species identified in the fish diets, with the difference again being largely attributable to the absence of *A. capensis*.

Total consumption by the six fish species was 5.99g $m^{-2}y^{-1}$, which was 30% of the production of the prey species consumed, or 17% of total secondary production within the weedbeds (Table 5). There was considerable variation in the intensity of predation on the different prey groups. Some 88% of the production of insect larvae, 86% of *Hymenosoma orbiculare* and 73% of *Corophium triaenonyx* was consumed suggesting that the fish are important predators of these prey. Conversely, the fish were only minor predators of *Ceratonereis erythraeensis*, *Cyathura estuaria*, *Apseudes digitalis* and *Callianassa kraussi*, consuming less than 2% of their production.

DISCUSSION

Consumption relative to production.

There is no general agreement concerning the ability of epibenthic predators to influence the community structure of their invertebrate prey in shallow-water soft-bottomed environments. Some studies suggest that predation has a marked effect, implying that prey species are in short supply (Virnstein, 1977; Riese, 1978; Summerson & Peterson, 1984), but others show the effects of predation to be minimal, suggesting that competition for food between predators is unimportant (McIntyre, 1973; Paine, 1980; Evans, 1983).

This study makes no attempt to assess the precise influence of predatory fishes in the Bot estuary on the structure of their prey populations. It is, however, possible to infer substantial influence in the case of species such as *Corophium triaenonyx*, *Hymenosoma orbiculare* and insect larvae which have large proportions (>73%) of their annual production consumed. The influence of fish predation on *Ceratonereis erythraeensis*, *Apseudes digitalis* and *Arcuatula capensis* (C = <1%P) is, however,

likely to be minimal. The average take of all prey species by the fish is 25%, which amounts to 17% of total invertebrate production, suggesting that the impact of fish predation is not likely to be great and that food is not in short supply. These findings agree with those of Evans (1984) who estimated that annual predation accounted for 24-34% of total macro- and meiofaunal production in Gullmar Fjiord (Sweden) and with Adams (1976) who obtained values of 19-21% for an estuarine eelgrass community. They support Choat (1982) who reviewed the effects of fish feeding on the structure of benthic communities and concluded that "predation by fishes may be difficult to demonstrate simply because it does not represent an important source of mortality in many prey populations".

In the same review Choat suggests that episodes of very high invertebrate mortality which are unrelated to fish predation may "obscure or render trivial mortality attributable to fish predators". Artificial breaching of the mouth of the Bot estuary has just such an episodic detrimental effect on the invertebrate community. De Decker (1987), who monitored one of these "unpredictable catastrophic events" showed that the number of species decreased from 23 to 15 and that the total biomass at his sites in the shallow *Ruppia* zone fell from $20gm^{-2}$ to $1.5gm^{-2}$ after the mouth was opened.

The effects of such major changes in the prey community on the fish can be evaluated because information is available on the species composition and biomass of the fish fauna immediately after the estuary was opened (Bennett *et. al.*, 1985)(Table 6). After breaching, the same six resident species considered in this paper still dominated the catch. Most occurred in greater densities than during the closed phase because they were concentrated into a smaller area by the receding water levels. If it is assumed that their daily consumption rates are the same before and after opening the estuary then, given a fish biomass of $0.744g\ m^{-2}$, consumption would have been $11.04g\ m^{-2}y^{-1}$. This is approximately double the rates of

consumption during the closed phase. Following breaching of the mouth prey biomass (estimated from de Decker, 1987) is reduced to about 2.50g m^{-2}. Using the assumption that the P/B ratio of the invertebrates is similar whether the estuary is closed or open, total prey production is calculated as 12.4g $m^{-2}y^{-1}$. Thus, during the period immediately after the estuary is opened, fish may consume approximately 90% of invertebrate production (Table 6) suggesting that they are having a marked effect on their prey populations and that competition for food among them is, for a brief period, likely to be intense. This situation is, however, never sustained as the mouth closes after a few weeks (Fromme, 1985).

Data are also available to evaluate the amount of prey production taken by fish in the nearby Palmiet estuary (34° 20'S, 18° 59'E). This estuary is normally open throughout the year and therefore is usually tidal and has limited weed growth. In this regard it is similar to the Bot when the latter is open. Data on the species composition, biomass and diets of fish in the Palmiet are available from Bennett (1989b,c) and measurements of invertebrate biomass and an estimate of invertebrate production are given by Branch and Day (1984). If it is assumed that the consumption rates of resident fish in the Bot and Palmiet estuaries are similar (which is reasonable since the two systems are dominated by the same resident species) then resident fish in the Palmiet will take 2.6% of the invertebrate production. This figure appears somewhat low in comparison with the Bot during its open phase but, in addition to the resident predatory fish, there are many juveniles of migrant species which enter the Palmiet from the sea (Bennett, 1989b). A large proportion of these are carnivorous (Bennett, 1989c). If these predatory migrants migrants are included then the consumption by the fishes rises to 8.7% of invertebrate production (Table 6), suggesting that competition for food is less in the open Palmiet estuary than it is in the Bot estuary during its closed phase.

Stability.

Bennett (1989b) has shown that in terms of biomass the percentage of resident species increases from 27% in the Palmiet through 33% in the seasonally open Kleinmond to 50% in the closed Bot estuary. In terms of their percentage contribution to numbers the increase in resident species is even more dramatic: 47% in the Palmiet, 81% in Kleinmond and 99% in the Bot.

This pattern may be explained by differences in stability between these systems. Estuaries which remain closed for prolonged periods (a number of consecutive years) have a low species richness and are therefore considered stressful environments (Whitfield, 1983) However, as far as the resident fish are concerned, such systems are stable and may offer advantages over open estuaries. For example, the Palmiet estuary which is open most of the time only remains open because of annual flooding. From this perspective it is unstable because the annual flushing causes massive scouring and short-term fluctuations in temperature and salinity. Flooding also prevents the establishment of weedbeds and maintains a low diversity of invertebrates (Branch & Day, 1984). Open estuaries such as the Palmiet also allow immigration of large numbers of marine migrant species many sharing the same food as the resident species and some preying upon them.

A system such as the Bot estuary is massively disturbed when the mouth is opened, especially by large reductions in the weedbed areas and in invertebrate biomass. Once it closes conditions stabilise. Weedbeds become established providing shelter for the resident fish and focal points for the concentrations of invertebrates - as has been documented for the Bot estuary by de Decker (1987). In this state there are no outflowing currents to export any of the productivity and the invertebrate populations rapidly attain high biomasses even though their diversity may be low. Populations of the resident fish species soon build up because they all reproduce during their first year of life (Bennett, 1989b). Migrant species are unable to breed

within closed estuaries so their numbers decline due to mortality once the mouth closes. Dietary overlap between residents and migrants is reduced as the migrants increase in size and vacate the shallow weeded margins for deeper water.

Thus a closed estuary may be more stable than an open system, seasonally open systems such as the Kleinmond are often of intermediate stability. Estuaries are however complex ecosystems, and their physical stability cannot be related in a simple manner to whether they are open or closed. Much depends on their seasonal and interannual variability, and to quantify their relative stabilty will require long-term monitoring. The approach we adopt here - of using estuarine stability as a means of predicting fish faunas warrants further exploration.

Niche dimensions.

Much ecological theory has been devoted to the concept that "niche apportionment" or "partitioning" of the habitat may prevent competitive exclusion (see Schoener, 1974; 1982; for reviews of this approach). The concept has frequently been applied to fish, and differences demonstrated between the habitats, diets or times of feeding of different species (e.g. Keast, 1970; Helfman, 1978; Macpherson, 1981; Evans, 1983; Gladfelter & Johnson, 1983). Whether these differences in niche dimensions are "used by fish to reduce competition and allow species to coexist" (Macpherson, 1981) is a moot point. Our results do not allow us to test the concept specifically, but they do bring into question the value of using niche breadths and overlaps to infer competition or an avoidance of competion.

In the first place, it seems likely that food is seldom limiting in either the Bot or the Palmiet estuaries, except perhaps for short periods of "crunch" (sensu Wiens, 1977), such as occur during the breaching of the Bot estuary, when invertebrate stocks are reduced and fish become concentrated.

Despite this, differences do exist between the six species considered. Feeding occurred at different times of the day (Figure 2). Niche breadths varied from highly specialised (*Syngnathus acus*: B=0.07) to generalised (*Atherina breviceps*: B=0.36) (Table 2). Dietary overlap between the species ranged from 0.121 to 0.493, based on the gravimetric contributions of different prey. Mean overlap (0.29) and mean niche width (0.17) were both more than the equivalent values measured by Macpherson (1981) for a guild of demersal predatory fish in the Mediterranean (0.17 and 0.11 respectively). This may reflect the need for broader diets in the physically more variable estuarine environment.

If specialization is to be effective in reducing competition, then it might be predicted that the dietary niche breadth of a species will be correlated with its average overlap with other species in a guild. Figure 3 shows that, although there is a trend in this direction, there is no significant correlation between the two within the resident species in the Bot estuary ($n=6$, $r=0.72$, $p<0.20$). If the data for dietary overlap are not averaged but replotted to show the relationship between the niche breadth of each species and its separate overlap with each other species, it becomes clear that overlap is greatest with the most abundant species (Figure 4). Indeed, all the resident species exhibited their greatest overlap with *Atherina breviceps*, which dominated the community by number (78%) and biomass (86%). In this light, specialisation amongst the fish of the weedbeds of the Bot estuary is a dubious option as a means of reducing competition.

Finally, amongst the six resident species, dietary niche breadth was directly correlated with abundance (Figure 5), implying that the most successful species are those with the broadest niches (whose diets incidentally overlap to the greatest degree with other species). A similar significant positive correlation between relative abundance and dietary niche breadth can be extracted from the data of Gladfelter and Johnson's (1983) study of tropical holocentrids ($n=6$, $r=0.87$,

$p < 0.05$) and a nonsignificant but positive relationship from Macpherson's (1981) study on demersal fish ($n = 26$, $r = 0.18$, $p < 0.50$). Thus the pattern may be general.

Specialisaion is often often held to be a recipe for extinction, especially under variable conditions (Gilpin & Soule, 1986), but if it is associated with small population sizes, this adds an additional risk in terms of the long-term survival of specialised species. Particularly in the context of the physical variability of estuaries, broad niches and adaptibilty may be the keys to success. Indeed, Bamber and Henderson (1988) have argued that the plasticity of the atherinids is the major reason they are so abundant in estuaries in many parts of the world. Although we cannot discount the possibility that niche specialisation reduces competition in the six species we have examined, the overall evidence suggests that a narrow niche is a disadvantage in estuaries.

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Table 1. Some ecological charactaristics of the fish community of the weed-bed areas of the Bot estuary. Feeding data are from Bennett (1989c) and all other information is from Bennett (1989b). Abbreviations c, d, o, h and p under diet stand for carnivore, detritivore, omnivore, herbivore and piscivore respectively and r, m and f indicate whether the fish are estuarine residents, marine migrants or freshwater species.

	Diet	life cycle	Occurr-ence %	Density N m^{-2}	%N	Mean individual mass g.
Atherina breviceps	c	r	100	1.715	78.7.	0.73
Gilchristella aestuaria	c	r	46	0.350	16.0	0.22
Psammogobius knysnaensis	c	r	77	0.051	2.3	0.67
Clinus spatulatus	c	r	64	0.034	1.5	2.17
Syngnathus acus	c	r	54	0.008	0.4	0.38
Caffrogobius multifasciatus	c	r	44	0.003	0.1	3.98
Liza richardsoni	d	m	18	0.019	0.9	4.70
Lithognathus lithognathus	o	m	10	0.001	0.1	1012.50
Mugil cephalus	d	m	8	< 0.0005	< 0.05	348.48
Hyporhamphus capensis	h	r?	5	"	"	5.00
Cyprinus carpio	d	f	8	"	"	423.08
Lichia amia	p	m	3	"	"	380.00
Oreochromis mossambicus	d	f	8	"	"	4.47
Rhabdosargus holubi	o	m	3	"	"	17.00

Table 2. The diets (% dry mass) and niche widths of the six fish species that are permanantly resident in the shallow weeded margins of the Bot estuary. Only food items that provided >1% of the diet of at least one species are included. (A.b. *Atherina breviceps*, G.a. *Gilchristella aestuaria*, P.k. *Psammogobius knysnaensis*, C.s. *Clinus spatulatus*, S.a. *Syngnathus acus*, C.m. *Caffrogobius multifasciatus*). Figures in bold highlight the groups contributing the major portion to each fish diet. Data from Bennett (1989c).

	A.b.	G.a.	P.k.	C.s.	S.a.	C.m.
POLYCHAETA	0.70	0.56	4.87	0.20		3.68
Capitella capitata	0.43		0.60			2.09
Ceratonereis erythraeensis			1.75			1.34
COPEPODA	2.32	16.98	4.39	0.26	**57.23**	0.08
Pseudodiaptamous hessi	1.06	4.76	1.16	0.26	36.54	
Harpacticoidea	0.47	0.35	1.04		4.62	
Calanoidea	0.46	10.17			10.31	
OSTRACODA	7.20	**32.55**	8.82	1.12	0.11	0.16
ISOPODA	20.17	0.41	6.08	33.68	15.44	11.79
Cyathura estuaria	0.39		0.14	0.50		7.50
Exosphaeroma hylecoetes	17.90	0.41	2.75	27.29	9.96	3.36
Munna sheltoni					1.04	
AMPHIPODA	**26.59**	5.48	18.44	14.16	24.32	8.33
Corophium triaenonyx	12.65	1.82	7.88	1.72	7.89	4.10
Grandidierella bonnieroides	3.20	0.24	0.98			0.11
Melita zeylanica	10.22	3.24	8.61	12.38	15.87	3.62
TANAIDACEA	0.11	3.71	0.39		0.08	1.73
Apseudes digitalis	0.11		0.32			1.57
DECAPODA	7.60		6.85			25.30
Callianassa kraussi	0.28		6.25			7.60
Hymenosoma orbiculare	6.70		0.48			15.69
AQUATIC INSECT LARVAE	16.24	15.53	**45.56**	3.47	2.49	14.63
Chironomidae	11.59	15.23	44.47	3.47	1.05	14.63
Diptera	1.98				0.19	
Odonata	2.65					
ADULT INSECTS	3.77	0.73	0.27	0.31		
Diptera	2.88	0.31	0.03	0.14		
GASTROPODA	9.95		0.90	**45.13**	0.42	
Hydrobia sp.	9.87	9.02	0.64	3.58	0.42	
Tomichia sp.			0.26	41.53		
PISCES	4.45	7.80	2.14	2.83		**34.27**
Atherina breviceps				2.75		22.14
Clinus spatulatus						8.97
eggs	2.93	3.66	2.09	0.08		
ALGAE	0.38	2.99	0.94	0.20		
Diatoms	0.03	2.99				
SPERMATOPHYTA	1.40	0.77	0.38	0.31		
Ruppia sp.	1.40	0.77	0.38	0.31		
NICHE WIDTH	0.36	0.26	0.10	0.15	0.07	0.10

Table 4. The feeding periods and durations, feeding rates (% body mass), average biomass (B, mg dry m^{-2}, from Bennett 1989 b) and total annual consumption (C, g m^{-2} y^{-1}) of six weed-dwelling carnivorous fish species in the Bot estuary.

	FEEDING PERIOD		FEEDING RATE		B	C
	Start-End	hrs.	h^{-1}	d^{-1}		
Atherina breviceps	1556-0044	8.8	0.56	4.93	283	5.09
Clinus spatulatus	0730-1848	11.3	0.51	5.63	16	0.33
Gilchristella aestuaria	0653-1659	10.1	0.56	5.66	19	0.40
Psammogobius knysnaensis	1948-0630	10.7	0.40	4.28	8	0.12
Syngnathus acus	0930-1920	10.5	0.38	3.76	1	0.01
Caffrogobius multifasciatus	0400-0824	4.4	0.53			
	1654-1920	2.4	0.47	3.48	2	0.03

Table 5. The standing stock (B, mg dry mass m^{-2}), mean mass at maturity (M_S, mg), estimated P/B ratios and total production (P, mg m^{-2} y^{-1}) of potential prey and amounts of each prey consumed by resident fish (C mg m^{-2} y^{-1}) in the Bot estuary. Figures for higher taxa are the sum of all species in each taxon including those listed separately.

	B	M_S	P/B	P	C	C/P (%)
POLYCHAETA	111	0.110	10.69	1186	46	3.88
Capitella capitata	29	0.084	11.81	342	23	6.86
Ceratonereis erythraeensis	54	0.140	9.77	528	2	0.40
COPEPODA	76	0.005	41.69	3168	198	6.26
OSTRACODA	100	0.008	35.03	3503	511	14.60
ISOPODA	1365	1.300	5.51	7520	1153	15.33
Cyathura estuaria	253	0.905	6.30	1594	24	1.50
Exosphaeroma hylecoetes	1112	1.534	5.18	5762	1009	17.50
AMPHIPODA	341	0.150	10.49	3578	1450	40.53
Corophium triaenonyx	57	0.048	16.00	912	669	73.36
Grandidierella bonnieroides	50	0.100	12.19	610	165	27.05
Melita zeylanica	226	0.250	8.69	1963	587	29.92
TANAIDACEA	67	0.092	14.19	951	21	2.20
Apseudes digitalis	67	0.092	14.19	951	6	0.67
DECAPODA	570	4.000	3.63	2070	403	19.49
Callianassa kraussi	470	4.593	3.45	1622	24	1.48
Hymenosoma orbiculare	100	3.000	4.04	404	347	85.90
INSECT LARVAE	58	0.047	18.80	1091	961	88.09
MOLLUSCA -	2842	27.500	2.78	7897	742	9.39
Arcuatula capensis	2573	41.225	2.39	6155	0	0.00
Hydrobia sp.	149	1.200	8.85	1319	551	41.78
Tomichia sp.	50	1.400	8.36	418	137	32.75
PISCES	1446	230.000	2.52	3644	281	7.71
Atherina breviceps	1248	200.000	2.64	3294	16	0.49
Clinus spatulatus	73	800.000	1.60	117	3	2.57
TOTALS	6976			34608	5766	

Table 6. Biomass, consumption and production in the Bot estuary during the closed and open phases and in the Palmiet estuary which is almost permanantly open.

	Bot closed	Bot open	Palmiet
Total carnivorous fish biomass ($g\ m^{-2}$)	0.33[a]	0.74[c]	0.18[a]
Biomass of resident fish ($g\ m^{-2}$)	0.33[a]	0.74[c]	0.05[a]
Biomass of prey ($g\ m^{-2}$)	6.98[b]	2.50[d]	14.70[e]
Production of prey ($g\ m^{-2}\ y^{-1}$)	34.61	12.40	38.52[e]
Consumption by fish ($g\ m^{-2}\ y^{-1}$)	5.99	11.04	3.36
C/P (%)	17.31	89.03	8.72

[a] Bennett (1989b), [b] de Decker and Bally (1985), [c] Bennett *et. al.* (1985), [d] de Decker (1987), [e] Branch and Day (1984).

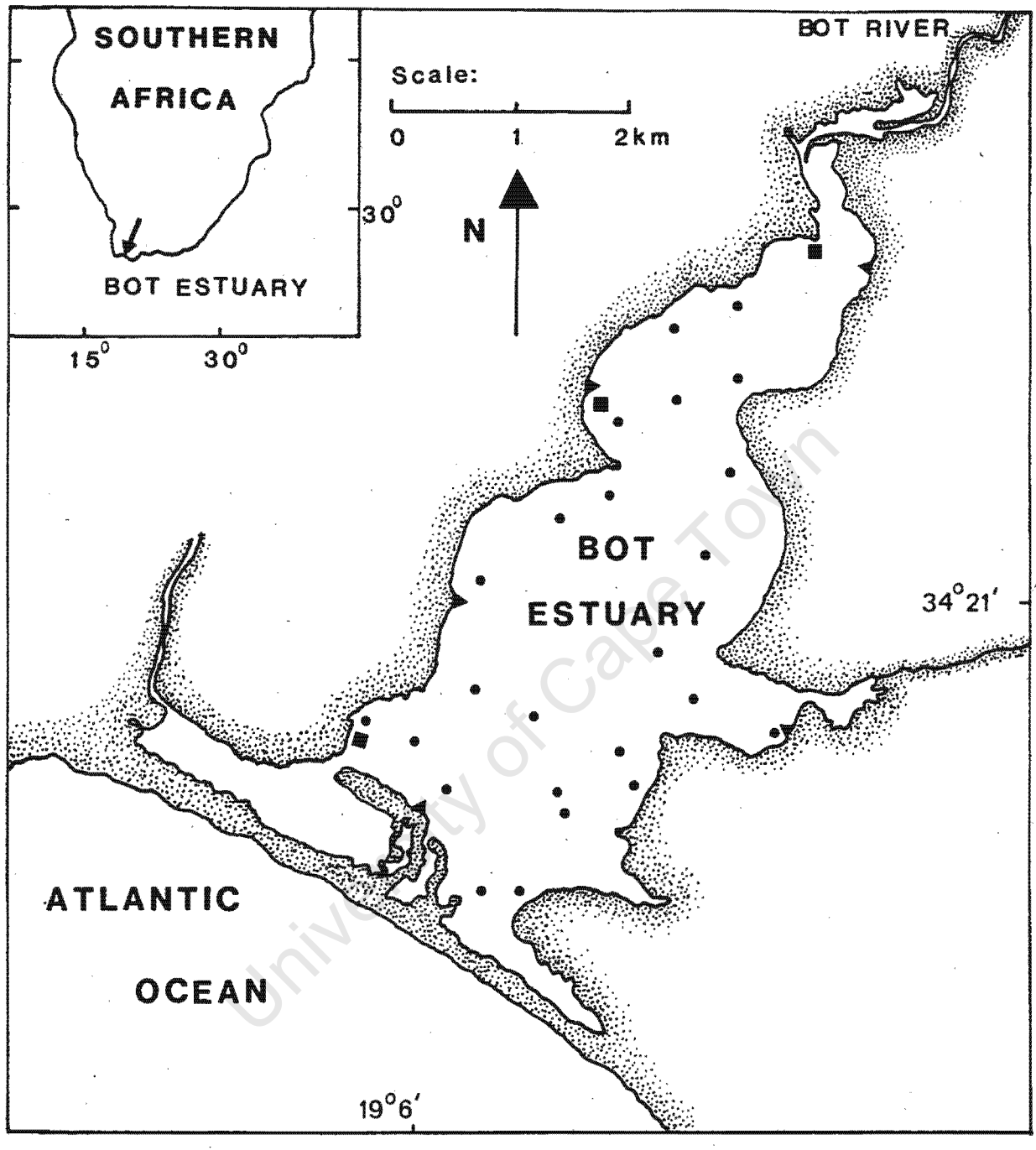

Figure 1. A map of the Bot estuary showing its position in southern Africa (inset) and the location of the sites at which the fish and invertebrate connunities were sampled. ■ indicates the positions of the fish sampling sites and ▶ and ● the sites sampled for invertebrates by Koop et. al. (1983) and de Decker and Bally (1985) respectively.

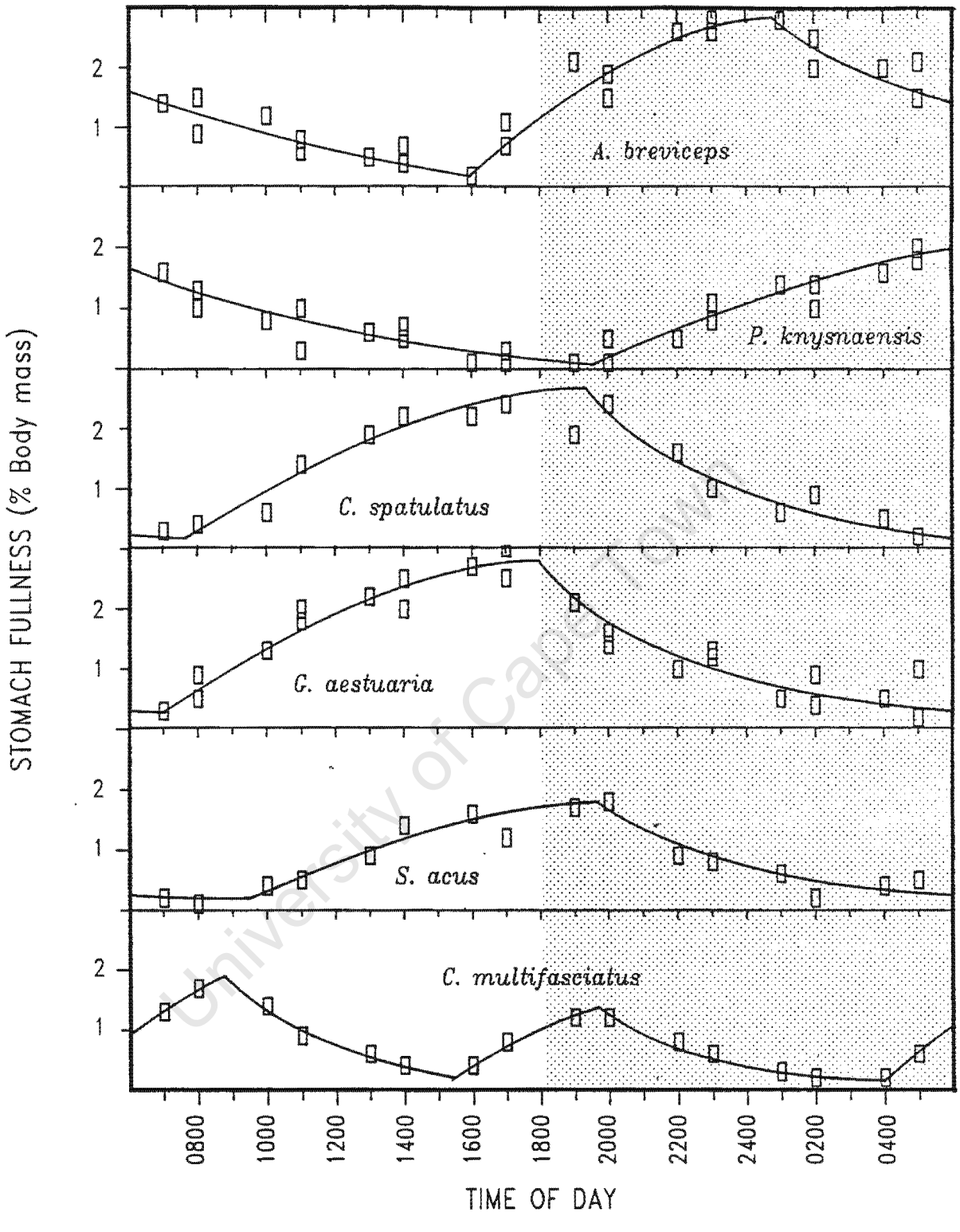

Figure 2. The feeding periods of six fish species resident in the weedbeds of the Bot estuary. Data points are the average amounts (% dry body mass) of food in the fish stomachs at 3-hourly intervals during three separate 24-hour sampling periods. Curves have been calculated from the Elliot and Persson (1978) model.

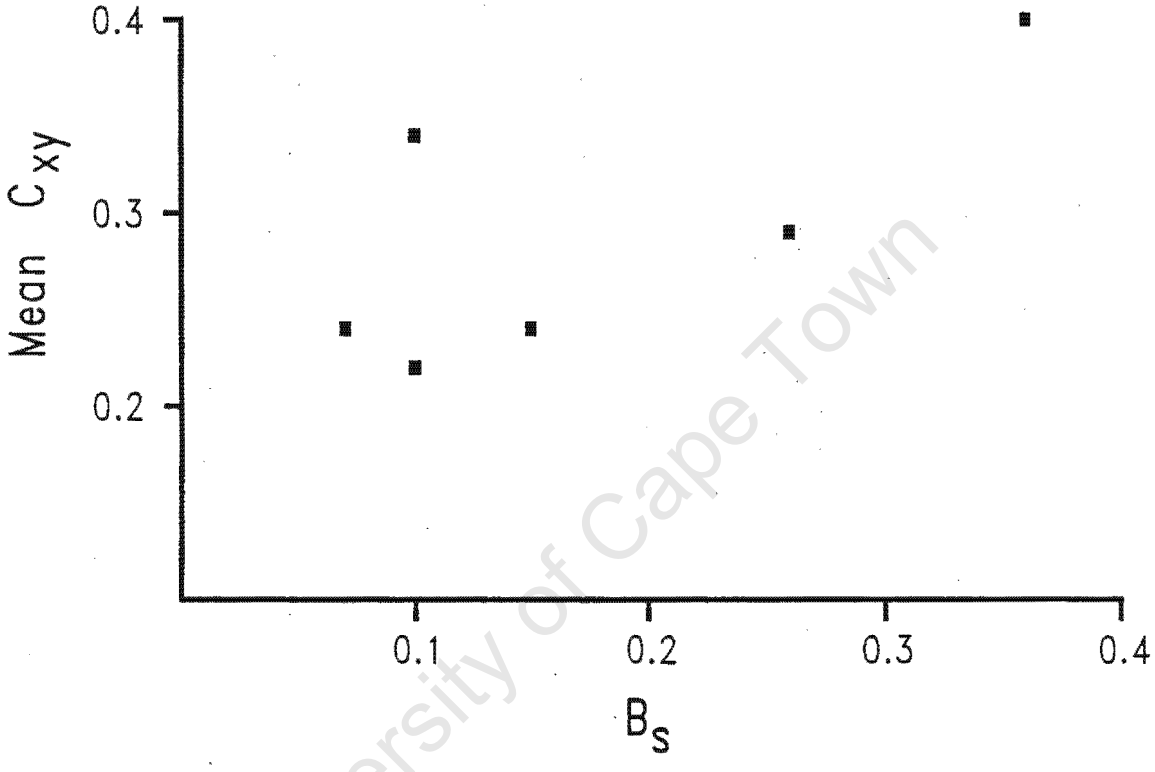

Figure 3. The relationships between the niche breadths (B_s) of each of the six fish species resident in the weedbeds of the Bot estuary and their mean overlap (C_{xy}) with each of the other five species.

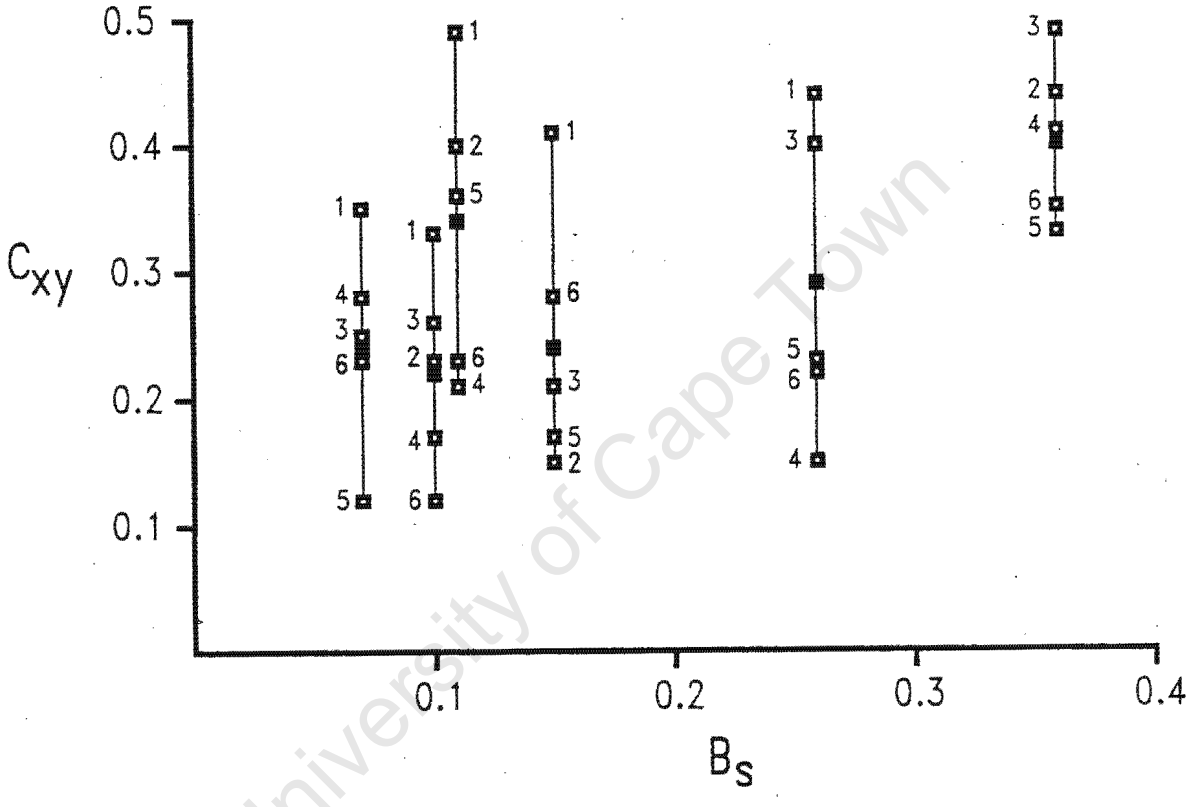

Figure 4. The relationship between the niche breadth (B_S) of each species and its overlap in diet (C_{xy}) with each of the other fish species resident in the weedbeds of the Bot estuary. Each species is numbered as follows: 1 *A. breviceps*, 2 *G. aestuaria*, 3 *P. knysnaensis*, 4 *C. spatulatus*, 5 *S. acus* and 6 *C. multifasciatus*. Solid symbols represent average overlaps.

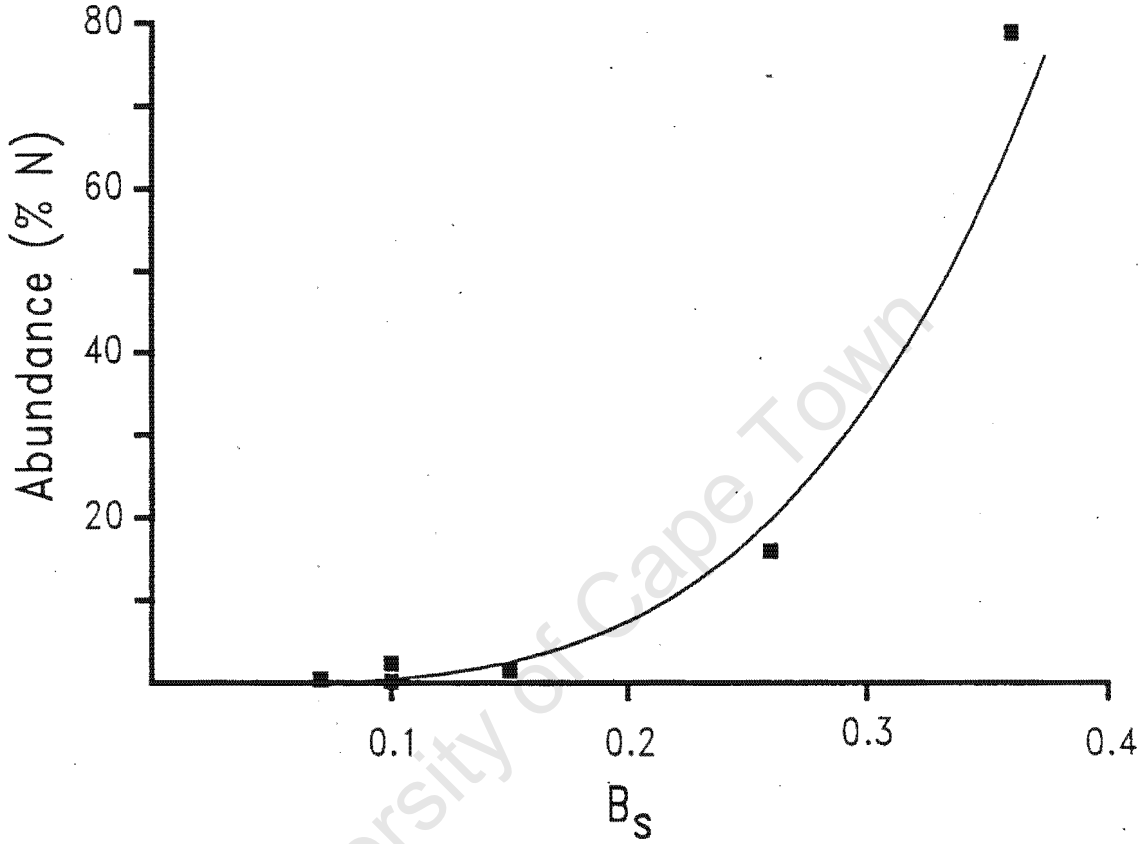

Figure 5. The relationship between the niche breadths (B_s) and relative abundances (A) of the six fish species resident in the weedbeds of the Bot estuary ($A = 3311.3\ B_s^{3.77}$, n=6, r=0.89).

OVERVIEW AND SYNTHESIS.

OVERVIEW AND SYNTHESIS

This overview provides a summary of the central findings presented in chapters 1-13 and synthesises the information to compare the three habitats sampled and the relative utilization of these habitats by fish. Table 1 summarises the nature and sources of this information. No new data are presented here but broad trends are extracted from the results in the earlier chapters. While most of the conclusions are drawn directly from these chapters the existing literature has been used to supply information on the seasonality of rock-pool fish and on the diets of surf-zone species.

Species, size composition and abundance

There were marked differences in the species composition of fish between the rocky intertidal, estuarine and surf-zone habitats sampled in the southwestern Cape during the course of this study (Chapters 1,5,6 & 7). None of the 21 species collected from rock-pools were found in either estuaries or the surf-zone and the latter two habitats shared only 10 of the 32 species seined there (Table 2). The fish in all three habitats were almost invariably small regardless of whether they were adults or juveniles, individuals in excess of 150 mm (T.L.) being unusual. In terms of the total number of species caught the three habitats were remarkably similar with 20-22 species occurring in each (Figure 1A). Despite this similarity in numbers of species the rocky shore community was considerably more diverse than the other two habitats having a Shannon-Weiner index of 2.1 as opposed to 1.1 in the estuaries and 1.4 in the surf-zone. This higher diversity is attributable to a more even distribution of relative abundance amongst the species. The rocky intertidal zone, however, supported fewest fish in terms of numerical density and had the lowest biomass.

Other major differences between the fish communities in these habitats involved the relative contributions of resident and non-resident species (Figure 1A). The majority of species on rocky shores in the southwestern Cape were residents *i.e.* they breed there and occur there as both adults and juveniles (Chapter 1). As one moves eastwards along the South Coast non-resident species become more important, especially in summer (Chapter 4). In the surf-zone, on the other hand, all but one of the species were non-residents, the majority occupying this habitat only as juveniles. Estuaries had intermediate numbers of resident and non-resident species. Similar trends emerge when the three habitats are compared in terms of the numerical density and biomass of resident and non-resident species (Figure 1B,C), the only major difference being that residents are numerically dominant in the estuaries even though the non-residents are considerably more important in terms of biomass. This is a consequence of the very small adult sizes of the estuarine residents.

Seasonality

No regular monthly sampling of the fish in rock-pools was undertaken in the southwestern Cape during this study thus there are no direct measurements of seasonal variation among these species in this geographic region. Quarterly sampling was however undertaken at Koppie Alleen on the South Coast (Chapter 4). From these samples and the literature there seems little doubt that seasonal and longer term variations in the populations of resident rock-pool fish are small. Further evidence for this is available from the work of Marsh *et. al.* (1978) and Butler (1981) who showed that individual fish exhibit a high fidelity to particular pools, and Penrith (1965) who observed that rock-pool fish tend to breed throughout the year. Bennett and Griffiths (1984) showed that the amount of rock cover available in pools is the most important factor governing the abundance and diversity of intertidal fish communities and Penrith (1970) and Beckley (1985)

Table 2. The relative abundance of different fish species occupying rock-pool, estuarine and surf-zone habitats in the southwestern Cape. **** indicates a contribution of >5% to the total number of fish caught, *** <5%->0.5%, ** <0.5%->0.1% and * <0.1%. A and J indicate whether adults and/or juveniles were sampled, and R indicates species that were permanantly resident in that habitat. Data are from Chapters 1, 5 and 6.

	ROCK-POOL		ESTUARINE		SURF-ZONE	
Caffrogobius caffer	****	AJ R				
Chorisochismus dentex	****	AJ R				
Clinus cottoides	****	AJ R				
C. superciliosus	****	AJ R				
Muraenoclinus dorsalis	****	AJ R				
Blennophis anguillaris	***	AJ R				
Cirrhibarbis capensis	***	AJ R				
Clinus acuminatus	***	AJ R				
C. agilis	***	AJ R				
C. heterodon	***	AJ R				
C. venustris	***	AJ R				
Halidesmus scapularis	***	AJ R				
Blennioclinus brachycephalus	**	AJ R				
Clinus berrisfordi	**	AJ R				
Eckloniaichthys scylliorhiniceps	**	A				
Galeichthys sp.	**	J				
Pavoclinus mus	**	AJ R				
P. pavo	**	AJ R				
Cheilodactylus fasciatus	*	J				
Clinus brevichristatus	*	A				
C. taurus	*	A				
Psammogobius knysnaensis			***	AJ R		
Clinus spatulatus			**	AJ R		
Liza dumerilli			**	J		
Mugil cephalus			**	J		
Myxus capensis			**	J		
Oreochromis mossambicus			**	AJ		
Syngnathus acus			**	AJ R		
Caffrogobius multifasciatus			*	AJ R		
Cyprinus carpio			*	J		
Diplodus cervinus			*	J		
Hyporhamphus capensis			*	AJ R		
L. tricuspidens			*	J		
Pomatomus saltatrix			*	J	***	J
Rhabdosargus globiceps			**	J	***	J
Atherina breviceps			****	AJ R	****	A
Liza richardsoni			****	J	****	AJ R
Gilchristella aestuaria			****	AJ R	*	A
Lithognathus lithognathus			***	J	*	J
Rhabdosargus holubi			**	J	*	J
Lichia amia			*	J	*	J
Sarpa salpa			*	J	*	J
Solea bleekeri			*	J	*	J
Lithognathus mormyrus					****	J
Diplodus sargus					***	J
Pomadasys olivaceum					***	J
Amblyrhynchotes honckenii					**	J
Cheilodonichthys capensis					**	J
Clinus latipennis					*	J
Heteromycteris capensis					*	J
Trachurus capensis					*	J
Sphyraena africana					*	J
Umbrina canariensis					*	J

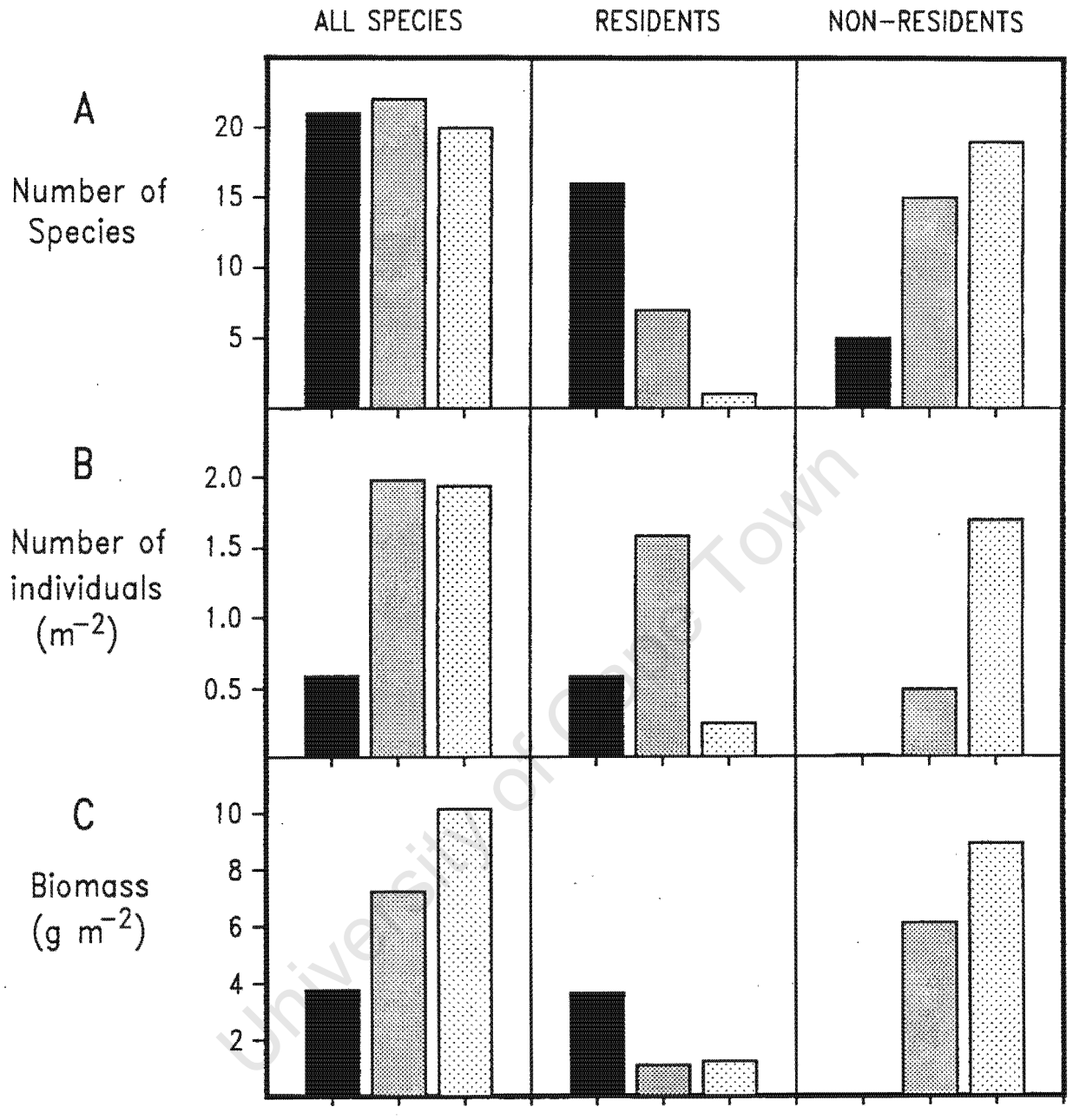

Figure 1. The number of species (A), number of individuals (B) and biomass (C) of all fish, and of residents and non-residents separately, in rock-pool ■, estuarine ▒, and surf-zone habitats ▒ in the southwestern Cape.

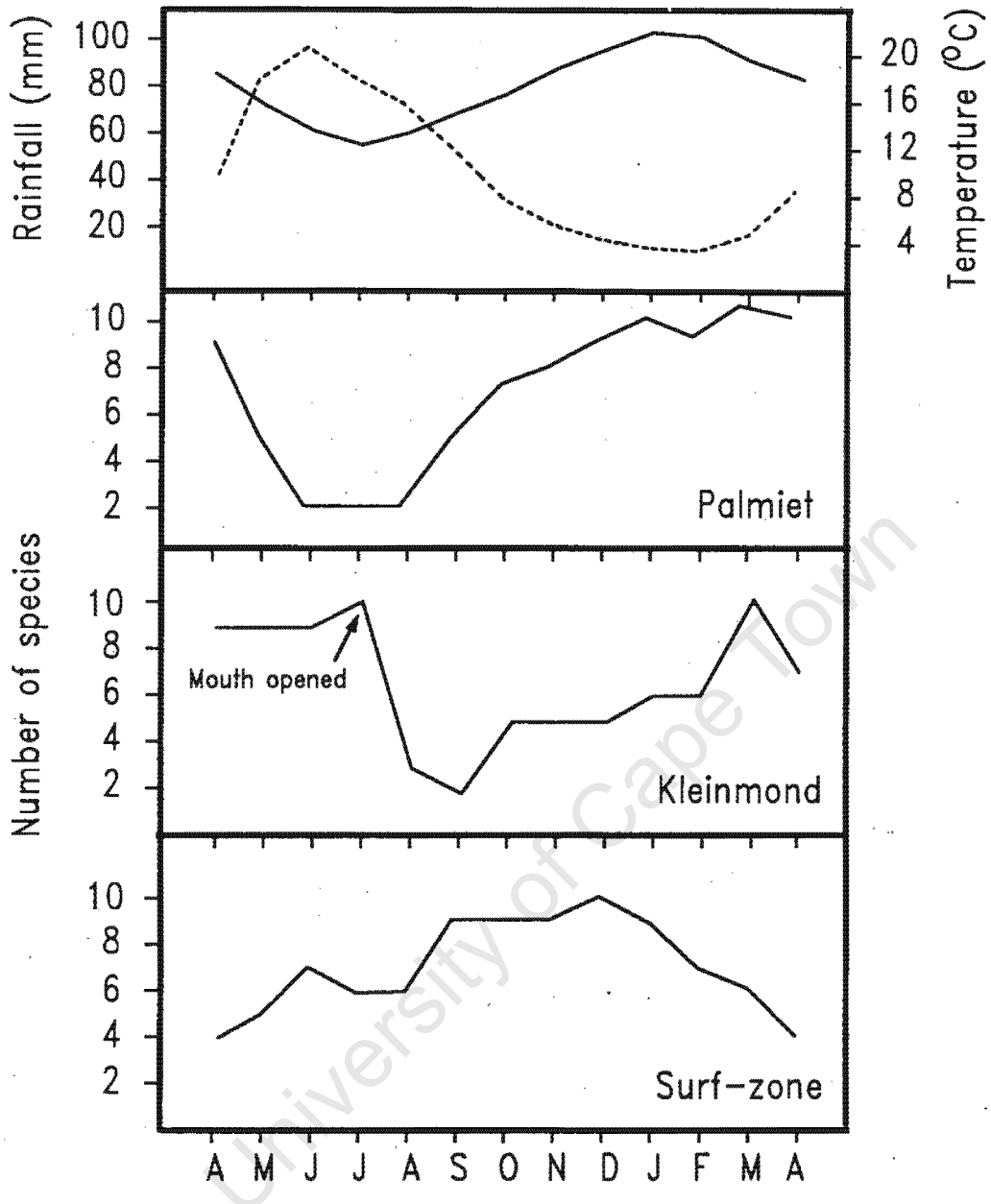

Figure 2. Seasonal variation in temperature (——) and rainfall (---------) in the southwestern Cape (from Heydorn and Tinley 1980), and in the number of species occuring in monthly samples from the Palmiet and Kleinmond estuaries (data from Chapter 6) and in the surf-zone (data from Chapter 5).

Table 1. A summary of the sources and nature of the information used in the overview and synthesis. Numbers indicate the chapters in this thesis from which data were obtained.

	Rocky Shore Intertidal	Estuaries	Sandy Beach Surf-zone
Species Composition	1	6	5
Size Composition	1	6,7	5
Seasonality	4	6,9,10	5
Diets	2	11	Derived from literature
Impact on Prey	3	13	not addressed
Habitat Utilization	1,3,4	6,8,9,12	5

demonstrated that after rock-pools are cleared of fish they may remain unoccupied for at least six months and that recolonisation is very slow.

The apparent stability of rock-pool fish communities is in marked contrast to estuaries and the surf-zone where there is considerable seasonal variation in the fish (Figure 2, and Chapters 5 & 6). The number of species in the Palmiet and Kleinmond estuaries ranged between a minimum of two in the winter and a maximum of eleven during the summer. The winter declines were closely associated with the onset of the rainy season which results in high freshwater input, reduced temperatures and floods which scour the estuaries and may even lead to mass mortalities of fish (Chapter 10). At this time the majority of fish species vacate the estuaries for the open sea. Most species occupying estuaries breed during the winter and spring months (Chapter 6). Thus, in the late spring and early summer when the rains have abated but the estuary mouths are still open, small juveniles of these species are available to recruit into the estuaries. There was little variation in the fish community of the Bot estuary during the year that it was sampled because it did not open to the sea. In years that it does open the pattern described above for the Palmiet and Kleinmond estuaries applies (Chapter 9).

The seasonal cycle in the surf-zone (Chapter 5) was not as strong as in the estuaries. Nevertheless, twice as many species were caught in this habitat during the summer as during the winter months (Figure 2). Thus, seasonal variation was characterised by different species exhibiting different patterns of abundance. Four species were caught throughout the year, two of them showing a summer peak in abundance and the other two having no clear cycle. Seven species occurred seasonally *i.e.* they were present for between three and six consecutive months and then disappeared. The seasonal cycles of these species were, however, not synchronised as different species occurred at different times of the year. A further nine species occurred sporadically and in low numbers.

Diets

The diets of fourteen estuarine fish species were examined in detail (Chapter 11). The small juveniles of all species consumed primarily zooplankton before switching diet, seven of them becoming carnivores which fed primarily on invertebrates, whereas two species became piscivorous, two herbivorous and three omnivorous. The diets of the four common mullet species were not examined but there is a considerable amount of published information indicating that they are all detritivores (Blaber 1976,1977; Blaber & Whitfield 1977; Masson & Marais 1975; Whitfield 1980; Whitfield & Blaber 1978). It is clear that the estuarine fish are collectively utilizing the entire spectrum of available food types. In the three estuaries considered there were three primary sources of food, *i.e.* phytoplankton, aquatic macrophytes and detritus. None of the fish examined consumed significant amounts of phytoplankton although this food source may have been of some importance in supporting the fry of all species via zooplankton. Macrophytes were consumed directly only by the two rare herbivores although they formed a significant proportion of the diets of the three omnivores. The bulk of the fish population - in terms of numbers of species, numbers of individuals and biomass - consumed benthic invertebrates, although small juveniles of most species consumed zooplankton.

The diets of the species constituting the intertidal rocky-shore fish community were remarkably uniform (Chapter 2). Nineteen of the twenty species that were examined were consumers of invertebrates and the remaining species was omnivorous, consuming both invertebrates and algae. This is in stark contrast to the situation in estuaries where diets of the same number of fish species were subdivided among five trophic categories. The intertidal food chain leading to the fish also differed from that in estuaries in that it was not primarily detritus-based. Most of the invertebrates consumed by the fish were polychaetes, amphipods,

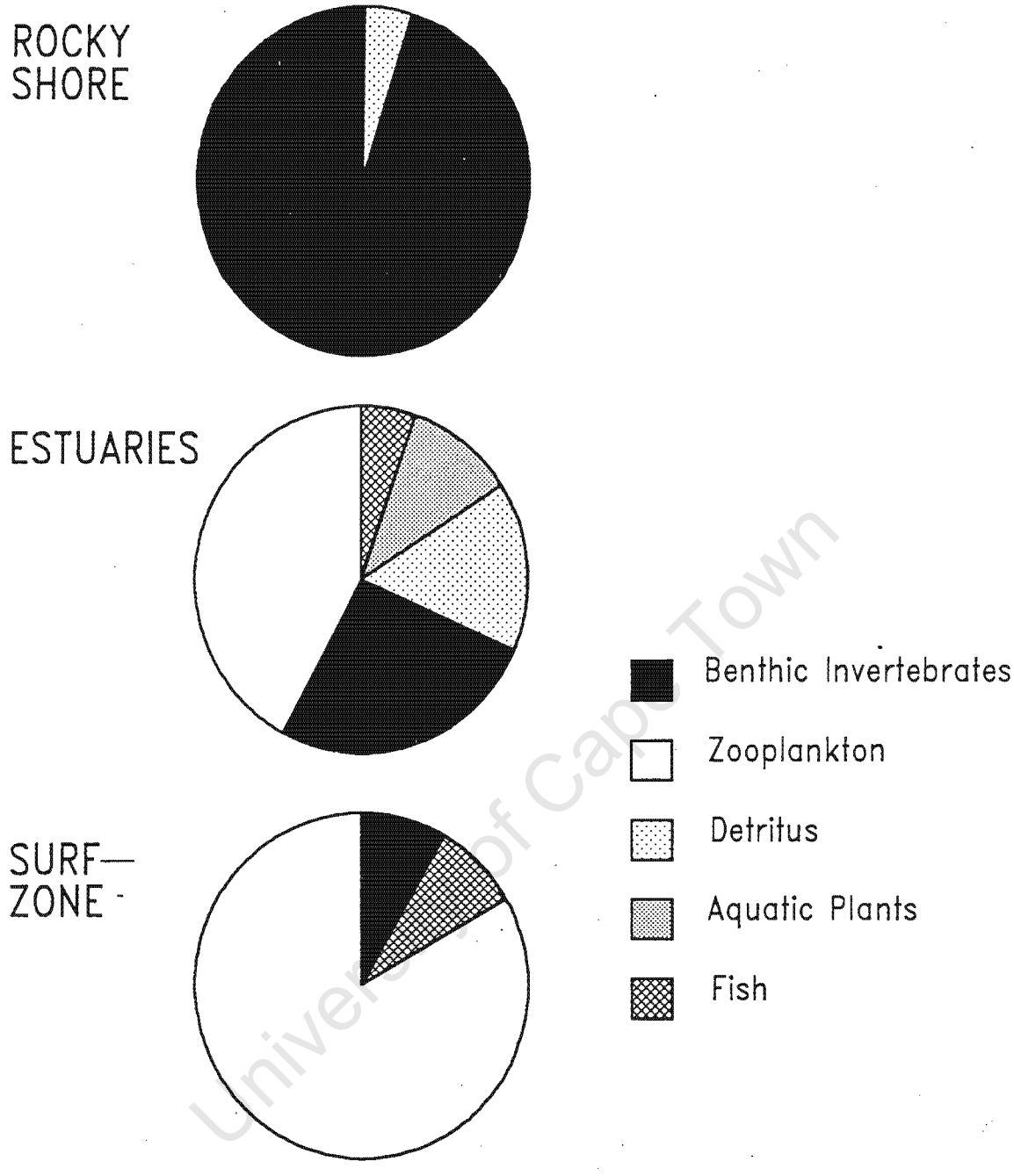

Figure 3. Proportions of the different food categories in the diets of fish in rocky-shore, estuarine and surf-zone habitats in the southwestern Cape as reflected by the numbers of species consuming each category. Data are from Chapter 2 (rocky-shore), Chapter 11 (estuaries) and Lasiak (1982, surf-zone).

isopods and small gastropods, classified by Branch and Griffiths (1988) as "small browsers", which consume seaweed or algal sporelings. Algae thus appear to underpin the food web supporting rock-pool fish.

The diets of surf-zone fish were not analysed in this study. The observations of Lasiak (1982) who described the diets of surf-zone fish in the eastern Cape are, however, relevant because the southwestern Cape surf-zone fish fauna is very similar to that in the southeastern Cape. She showed that the food base of the surf-zone fish is primarily zooplankton, with infaunal invertebrates being only of minor importance. She also showed that species which consumed detritus or benthic infauna in estuaries relied primarily on planktonic invertebrates when in the surf-zone.

Thus, in terms of their food resources, the fish communities of the surf-zone, estuaries and rocky-shores are radically different. Estuarine fish use a wide spectrum of trophic types and their food web is ultimately based largely on detritus. Surf-zone fish feed almost entirely on zooplankton whereas rock-pool fish virtually all consume benthic invertebrates and depend on a food web based on living seaweeds (Figure 3).

Subdivision of the food resource

The co-habitation of a large number of species in the intertidal zone of rocky shores, all of which consume benthic invertebrates, suggests that competition for food will occur. Despite the substantial dietary overlap between the species there is, however, considerable subdivision of the food resource (Chapter 2). Not all the species rely on the same dietary categories to the same extent and many of the species consume food types unimportant in the diets of the other species. Differences in mouth size of the fish species and changes in diet during growth are

also associated with differences in the size and species composition of their prey. The food resource is further subdivided by virtue of the fact that the fish species do not have identical habitat requirements even though they may occur in close proximity with one another. For example, differences in vertical distribution, in the preference for weeded or non-weeded areas, and in size and body shape will result in different species of fish feeding in different micro-habitats.

In contrast to the situation on rocky shores where all but one of the species was carnivorous, the estuarine fish species consumed food drawn from five trophic categories (Chapter 11). Resource subdivision within four of these trophic categories was not analysed because there were only a few fish species in each. The six resident species which dominated fish numbers and biomass in the shallow weedbeds were, however, all carnivorous. Although there was considerable overlap in diet between these species they subdivided their invertebrate prey resource by specialising on different prey categories, by feeding at different times of the day and by exploiting different micro-habitats (Chapter 11). The demonstration of dietary resource partitioning is, however, not in itself evidence that the fish are competing, nor can it be assumed that partitioning serves the purpose of reducing competition. The extent to which different species may be competing can, however, partially be determined from their impact on food resources, as outlined below.

Impact on the food resource

Annual consumption of invertebrates by the rock-pool fish community amounted to 17.9 g m^{-2} of shore area (Chapter 3). This represented 0.76% of the total annual production of invertebrates on the shore. Much of this total production was, however, attributable to organisms which are never consumed by the fish. Almost the entire predation pressure was borne by small mobile crustaceans, polychaetes and molluscs which together comprised only 3.7% of total production. The fish

consumed 64% of this "available" production. Thus, whereas rock-pool fish probably have a neglible effect on the intertidal benthic community as a whole, their influence on specific species may be substantial.

Three estimates of the impact of estuarine fish on their prey were made (Chapter 13). In the Bot estuary during its closed phase, the weedbed fish community consumed an estimated 17% of total secondary production or 30% of prey production. However, when the estuary was open the fish consumed approximately 90% of total production. This marked increase was attributed to the fact that the fish were concentrated in a smaller area by the reduced water level thereby increasing their density. At the same time invertebrate biomass was reduced by the scouring effect of the rapid outflowing currents when the mouth was breached. In addition the weedbeds, in which the majority of the invertebrates lived, were stranded by the receeding water levels. The fish in the Palmiet estuary apparently had only a minor impact on the production of their prey, accounting for only 8.7% of invertebrate production.

From the above it appears that food is seldom limiting in the estuaries, whether they are open or closed, except for brief periods such as occur in the Bot estuary immediately after breaching, when invertebrate stocks are reduced and the fish become concentrated. In view of this, niche apportionment appears to be of questionable value either in reducing competition or in allowing the different species to co-exist. If specialization were to be effective in reducing competition then it might be expected that the dietary niche breadth of a species would correlate with its average overlap with other species in a guild. In the case of carnivorous residents in the weedbeds of the Bot estuary (Chapter 13) there was no such correlation. In fact, overlap was usually greatest with the most abundant species and niche breadth was directly correlated with abundance. In this light, specialization appears to be a dubious means of reducing competition.

Habitat utilization

Most of the fish species inhabiting estuaries in the southwestern Cape can be classified as either residents or migrants depending on their patterns of reproduction and recruitment (Chapters 6 & 9). All the resident species have some reproductive specialisation that enhances the retention of eggs within estuaries (Chapter 6). For example, one species is ovoviviparous, one retains eggs and larvae within a brood pouch and four lay large eggs which have threads to facilitate attachment to some fixed substratum. Loss of eggs to the sea by these species is further reduced by the fact that all but one of the species breed during the summer when rainfall is negligible and most of the estuaries are closed or, if open, water currents are at a minimum. For resident fish, further advantages of summer spawning are that aquatic macrophytes and invertebrate populations will have recovered from stranding and scouring of the previous winter by the time that hatching occurs. Maximum cover and food are available and high temperatures prevail, all conditions that will optimise growth of larvae and juveniles.

Thirteen migrant species of marine origin were sampled in the southwestern Cape estuaries. In the estuaries that were open to the sea for some part of the year the overwhelming majority of the migrants were juveniles of less than one year old . In contrast to the residents, the migrant species spawn in the sea primarily during the winter and spring months and small juveniles (usually 20-60mm T.L.) enter the estuaries during the spring and summer approximately 2-4 months after spawning (Chapter 6). Recruitment therefore takes place after the rainy season but before the estuaries close. They remain in the estuaries, where they benefit from the favourable conditions throughout the summer and autumn, before returning to the sea at the onset of the following winter. The condition of one species, *Liza*

richardsoni, has been shown to be better in estuaries than in the marine environment (Chapter 12).

From the above accounts it appears that the fish community of the estuaries in the southwestern Cape is governed primarily by the marked seasonal cycle in physical conditions that occur there. The reproductive cycles of the fish species that utilize these estuaries seem adapted to seasonal variations in these estuaries. Favourable conditions, however, occur only during the summer months. During the winter rains the estuaries receive cold, low salinity water and are frequently scoured by floods. The juvenile migrant species avoid these adverse conditions by vacating the estuaries during winter for the sea. The benefits offered by the estuarine nursery to the migrants during their first summer appear, however, to be so great that a number of the species are entirely or partially dependent on estuaries during this phase of their life cycles (Chapter 8).

The surf-zone, being on the fringe of the greater inshore marine environment, is buffered from many of the seasonal physical changes that are experienced in estuaries and, since it is not enclosed in any way, fish are able to move freely in and out of the habitat. Despite these two factors there were still significant seasonal variations in the surf-zone fish community, with peak numbers of species being present during the summer months (Figure 2). Some species exhibited seasonal peaks of abundance, whereas others were only present at particular times of the year (Chapter 5).

The shallow surf-zone area was inhabited almost exclusively by non-resident species the majority of which were represented by small juveniles. Possible reasons why small fish frequent this habitat include warmer temperatures and protection from predators due to wave action and increased turbidity. Larger piscivorous fish are not common in the shallows of the surf zone. The abundance of juveniles of many

species in the surf-zone relative to other habitats suggests that the surf-zone is an important nursery habitat. A large proportion of these species may be dependent on this nursery (Chapter 5).

The rock-pool habitat on southwestern Cape shores is occupied almost exclusively by cryptic, benthic species which have morphological, reproductive, physiological and behavioural adaptations that enable them to remain permanantly resident on rocky shores (Gibson 1969, 1982). The critical factors limiting the abundance and diversity of this community appear to be the physical characteristics of rock-pools (Chapter 1). Two lines of evidence support this conclusion. Firstly, there is no significant difference in the densities of fish inhabiting similar pools between areas where the number of pools per unit of shore area is different. The carrying capacity of the pools, rather than food availability in the surrounding area, is therefore likely to be limiting. Secondly, there is not enough food available in the rock-pools to sustain the resident populations. To meet the energetic requirements of the fish tidepools would need to have approximately 400 g m^{-2} of their prey species. Over the entire shore the biomass of prey is only 11 g m^{-2} (Chapter 3). Much of their food must therefore be obtained from outside the pools while foraging during high tide. During low tide, however, all the intertidal residents were confined to rock-pools. Competition for shelter within rock-pools is therefore likely.

The amount of rock cover available in the pools proved to be the most important of the environmental variables accounting for the observed variance in the abundance, diversity and biomass of the fish populations (Chapter 1). The importance of rock cover was attributed primarily to the protection that it provides from predators and wave turbulence. Increased rock cover may also have increased the number of microhabitats available for different species but this possibility remains to be tested and can only be inferred from the morphological diversity of fish within rock-pools.

The confinement of intertidal fish to rock-pools and the correlation of fish numbers, biomass and diversity with rock cover all suggest that pools with adequate cover are the single most important factors controlling fish populations on rocky intertidal shores. Rock-pools are essentially constant in time and fixed in space. They therefore impose restrictions on the movements of resident fish. This is reflected in the very slow recovery of pools denuded of fish. This environmental constancy is in strong contrast to the variability exhibited by estuaries. The limited area and fixed spatial distribution of rock-pools are, likewise, a contrast with the sandy beach surf-zone. Given these circumstances it is logical that rock-pool residents breed year round and show little seasonal variation in numbers and species composition (Chapter 4).

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